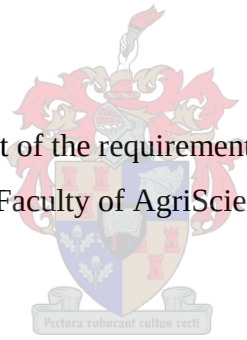
Distribution and impact of the Argentine ant, *Linepithema humile* (Mayr), in South Africa

Ndivhuwo Mord Luruli



Thesis presented in partial fulfillment of the requirements for the degree of Master of Science (Conservation Ecology), in the Faculty of AgriSciences, University of Stellenbosch

Supervisor: Professor M.A. McGeoch

March 2007

DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature: _____

Date: _____

ABSTRACT

Invasion by the notorious tramp species, the Argentine ant (*Linepithema humile* Mayr) (Hymenoptera: Formicidae) has caused major concern around the globe, owing to its displacement of native ant species and other invertebrates where it invades. This species was first recorded in South Africa in 1901 in Stellenbosch, Western Cape Province (WCP), and has now become a significant pest in most urban and agricultural areas in the country. The Argentine ant has received relatively little attention in South Africa compared to other countries (e.g. California, North America). To date the extent of invasion by this species countrywide, as well as its impact on the local ant fauna inside protected areas, has not been quantified. In this study, the impact of the Argentine ant on native ant fauna inside three protected areas in the WCP (Helderberg Nature Reserve (HNR), Jonkershoek Nature Reserve (JNR) and Kogelberg Biosphere Reserve KBR)) was assessed. Species richness and diversity were compared between invaded and uninvaded bait stations at each protected area. Several native ant species were found to be displaced by the Argentine ant from all three protected areas, although three species: *Meranoplus peringueyi*, *Monomorium* sp. 8 and *Tetramorium quadrispinosum*, were found coexisting with it. Invaded bait stations had significantly lower ant species richness and species turnover than uninvaded bait stations. Uninvaded bait stations contained eight times more native ant species than invaded bait stations. Thus, the invasion of protected areas by the Argentine ant has severe negative consequences for the species richness and assemblage structure of native ants, leading to the biotic homogenization of these local ant communities. The distribution range of the Argentine ant inside the three protected areas (HNR, JNR, KBR), as well as microhabitat preferences that may facilitate the spread of this species inside these reserves, was also assessed. Helderberg Nature Reserve was the most invaded protected area, with the highest level of the Argentine ant occupancy, while JNR and KBR had lower occupancy levels. At all the three protected areas, this species was dominant at lower altitudinal areas, and also showed a clear preference for areas with high anthropogenic disturbances, i.e. around buildings and on lawns (picnic areas). In this study, there was no evidence that moisture availability facilitates the distribution and spread of the Argentine ant inside these reserves. Finally, a

combination of published literature records, museum records and records collected in the current study was used to quantify the current distributional extent of the Argentine ant throughout urban South Africa. This is the first study quantifying the distribution and extent of invasion by the Argentine ant throughout the country. The Argentine ant was found in six of the nine South African Provinces, and its extent of occurrence includes approximately half of the country's land surface area. Discontinuities in the distribution of the Argentine ant across the country revealed that range expansion of the Argentine ant in South Africa is occurring predominantly via human-mediated jump dispersal, rather than naturally via nest diffusion. This study clearly demonstrated that the Argentine ant is well established across South Africa as well as inside protected areas. The Argentine ant invasion was influenced by the presence of human modified landscapes (i.e. buildings) both at low and high altitude, and this was associated with higher rates of native ant species displacement at these areas. Therefore, limiting the development of recreational areas, such as buildings and picnic sites inside protected areas will result in the lower rate of spread of the Argentine ant. This will in turn lower the extent of displacement of native ant species.

OPSOMMING

Indringing deur die Argentynse mier (*Linepithema humile* Mayr) (Hymenoptera: Formicidae) is ‘n bron van groot kommer regoor die wêreld, as gevolg van sy vermoë om inheemse mier spesies en ander ongewerweldes te verplaas. Hierdie spesie is vir die eerste keer aangeteken in Suid-Afrika in 1901, in Stellenbosch, Weskaap Provinsie (WCP), en het ‘n belangrike pes geword in die meeste stedelike en landelike gebiede in die land. Die Argentynse mier het betreklik min aandag gekry in Suid-Afrika, in vergelyking met ander lande (bv. California, Noord Amerika). Tans is die omvang van die landwye indringing van hierdie spesie, sowel as sy impak op die plaaslike mier fauna binne beskermde areas, nog nie bepaal nie. In hierdie studie word die impak van die Argentynse mier op die inheemse mier fauna binne drie beskermde areas in die WCP (Helderberg Natuurreservaat (HNR), Jonkershoek Natuurreservaat (JNR) en Kogelberg Biosfeerreservaat (KBR)) bepaal. Spesierykheid en diversiteit was vergelyk tussen ingedringde en oningedringde lokaas stasies in elke beskermde area. Verskeie inheemse mier spesies was deur die Argentynse mier verplaas in al drie beskermde areas, alhoewel drie spesies: *Meranoplus peringueyi*, *Monomorium* sp. 8 en *Tetramorium quadrispinosum* het saam met dit voorgekom. Ingedringde lokaas stasies het beduidend laer mier spesierykheid en spesies omset gehad as oningedringde lokaas stasies. Dus, die indringing van beskermde areas deur die Argentynse mier het ernstige negatiewe gevolge vir die spesierykheid en gemeenskap struktuur van inheemse miere, wat lei tot die biotiese verarming van hierdie plaaslike mier gemeenskappe. Die verspreidingsarea van die Argentynse mier binne die drie beskermde areas (HNR, JNR, KBR), en die mikrohabitat voorkeure wat die verspreiding van die spesie binne hierdie reservate kan vergemaklik, was ook vasgestel. Helderberg Natuurreservaat was die mees ingedringde beskermde area, met die hoogste vlak van Argentynse mier besetting, terwyl JNR en KBR laer besettingsvlakke gehad het. By al drie die beskermde areas was hierdie spesie dominant by laer hoogtes bo seevlak en het ‘n duidelike voorkeur getoon vir areas met hoë menslike versteuring d.i. rondom geboue en op grasperke (piekniek areas). In hierdie studie was daar geen bewyse dat vog beskikbaarheid die voorkoms en verspreiding van die Argentynse mier binne die reservate vergemaklik nie. Ten slotte, ‘n kombinasie van

gepubliseerde literatuur verslae, museum dokumente en verslae wat in hierdie studie versamel is, was gebruik om die huidige verspreidingsomvang van die Argentynse mier te bepaal. Dit is die eerste studie wat die verspreiding en omvang van indringing in stedelike Suid Afrika van die Argentynse mier dwarsdeur die land bepaal. Die Argentynse mier is gevind in ses van die nege provinsies in Suid-Afrika, en die omvang van sy voorkoms sluit bykans die helfte van die land se landoppervlaksarea in. Onderbrekings in die verspreiding van die Argentynse mier deur die land het blootgelê dat die uitbreiding van die voorkomsgebied van die Argentynse mier in Suid-Afrika hoofsaaklik gebeur deur mens bemiddelde verspreiding eerder as natuurlike nesverspreiding. Hierdie studie het duidelik gedemonstreer dat die Argentynse mier goed gevestig is regoor Suid-Afrika sowel as in beskermde areas. Die Argentynse mier indringing was beïnvloed deur mensgewysigde landskappe (d.i. geboue) by lae en hoë hoogtes bo seevlak, en dit was verwant aan hoër vlakke van verplasing van inheemse mier species in hierdie areas. Dus, die beperking van ontwikkeling van rekreasie areas, soos geboue en piekniekareas, in beskermde gebiede sal lei tot laer vlakke van verspreiding van die Argentynse mier. Dit sal, op sy beurt, die omvang van verplasing van die inheemse mier spesies verminder.

DEDICATION

To my husband, **Nyambeni**……

I couldn't have possibly done this without your constant understanding and support, I will be eternally grateful!

I love you

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to my Supervisor, **Prof. Melodie A. McGeoch** for her support and encouragement throughout this project, and for believing in me. Prof, thank you for being such an inspiration.

The financial support of **The Andrew Mellon Scholarship** and **DST/NRF Center for Invasion Biology** is greatly acknowledged.

Thank you to the manager of Helderberg Nature Reserve (**Mr P. Koker**), Jonkershoek Nature Reserve (**Mr. M. Wilmot**), and Kogelberg Biosphere Reserve (**Mr Mark Johns**) for allowing me to carry out this project in these reserves.

Thank you to **Dr. H.G. Robertson** of Iziko Museum, Cape Town, for supplying locality records; and also **Dr. Helen de Klerk** (Western Cape Nature Conservation Board (WCNCB), Scientific Services); Department of Geography, University of Stellenbosch, for providing GIS data.

Drs. **A. Botes** (University of Stellenbosch), **C.L. Parr** (CSIRO, Australia) and **B. Braschler** assisted with the identification of ant species, for which I am very grateful.

Thank you to all my field assistants, especially Ms. **Yolanda Wiese**. I would also like to thank Drs. **J. Kalwij**, **C. Hui**, & **R. Veldtman** for their help. To my lab colleagues: the past two years would be very boring without you guys! Thank you for being so supportive and always willing to help.

I am very grateful to Prof. **S.L. Chown**, Dr. **J. Terblanche**, **The Run Walk For Life** (Somerset West), and everyone who supplied ant samples from their homes and anywhere across South Africa: thank you for your contribution to this project, and to science. Chapter 4 in this thesis is dedicated to all of you!

A very special thank you to my parents (**Naledzani Suzan** and **Azwidivhiwi Solomon Netshilaphala**) for their support, encouragement, and for the sacrifices they made for me over the years. To my brother (**Hulisani**) and sisters (**Mulisa** & **Sechaba**): Thank you for being my inspiration! To all my friends, especially **Divhani Rammbuda** & **Ntanganedzeni Ranwedzi**: thank you for your friendship and prayers. Ntanga, you made my year!

Finally I would like to thank **GOD** for giving me the strength and courage to cope with all the challenges during this project. Lord I thank you for **Jeremiah 29 v 11.**

TABLE OF CONTENTS

CHAPTER 1

General introduction: Ants as invasive alien species

Biological invasion is the second most important threat to biodiversity in many parts of the world (Vitousek *et al*. 1996; Wilcove *et al*. 1998; Lee 2002; Von Aesch & Cherix 2005), following habitat destruction and degradation (Wilcove *et al*. 1998; Lee & Klasing 2004). Invasive alien species, i.e. non-native species that often cause economic or environmental damage in their introduced areas, are increasingly altering terrestrial and aquatic communities worldwide (Gurevitch & Padilla 2004). In some important cases, invasive species have negative impacts on the native ecological communities they invade (Hee *et al*. 2000; Stout *et al*. 2002), often causing dramatic changes in species composition of invaded communities (Fagan & Peart 2004). Invasive species not only affect ecosystem processes, but also the distribution and abundance of native species (Kennedy 1998). Single invasive species can threaten entire ecosystems (Samways 1996). For example, in 1990 alone, rice farmers in the Philippines lost up to $45.3 million as a result of invasion by the golden snail (*Pomacea canaliculata*), split among control costs and yield losses (Vitousek *et al*. 1997).

Several species of different taxa i.e. plants, animals, birds, as well as invertebrates, both marine and terrestrial, have been introduced into many parts of the world, and some have become invasive (Pimentel *et al*. 2001). The total number of introduced species in the United States, United Kingdom, Australia, South Africa, India and Brazil ranges from about 2000 to 50 000 species (Pimentel *et al*. 2001). Generally, there are more introduced plant species than introduced animals (Vitousek *et al*. 1996). Alien invasive plants can have many negative impacts on native communities (Lindenmayer & McCarthy 2001) through competition for resources (Walck *et al*. 1999), changing soil nutrient status (Rose & Fairweather 1997) and altering disturbance regimes such as fire (Mack & D'Antonio 1998). However, some small mammals have also caused significant impacts in their introduced areas. For example, the house mouse, *Mus musculus*, has been accidentally introduced to many sub-Antarctic islands, where it has become a significant predator of endangered and endemic seabirds (Cuthbert & Hilton 2004; Rodríguez *et al*. (in press)). Campbell and Atkinson (2002) also reported the effects of the Pacific rat, *Rattus exulans*, on some plant and animal species on New Zealand's northern offshore islands. Sometimes the presence of an invasive species can cause an increase of other invasive species of different taxa. For example, invasive plants can increase the abundance of invasive invertebrates in an area (*sensu* Lenz & Taylor 2001; Standish 2004). They can also reduce the abundance and species assemblage of native invertebrates

(Samways *et al*. 1996). Oceanic islands are particularly vulnerable to invasion by different taxa, i.e. alien microbes, fungi, plants and animals (Gremmen *et al*. 1998; Frenot *et al*. 2001, 2005; Cuthbert & Hilton 2004).

Although biological invasion has been regarded as a natural component of ecological communities over evolutionary time (Morrison 2000), the current rate of invasion is clearly a human-induced phenomenon (Rejmanek 1996). Humans are largely responsible for the transport of species beyond their native ranges, both deliberately and accidentally, and many of these alien species become established and continue to spread in their new habitat (Holway 1995; Vitousek *et al*. 1997; Ward *et al*. 2005). Activities such as agriculture, aquaculture, recreation, tourism and trade promote both the intentional and accidental spread of invasive species across different areas (Vitousek *et al*. 1997; Kolar & Lodge 2001; Mack & Lonsdale 2001; Lake & Leishman 2004; Maki & Galatowitsch 2004; Knowler & Babier 2005; Margolis *et al*. 2005; Perrings 2005).

Invasive insect species

Of the many invading organisms, insects are among the most detrimental to human health, (e.g. the invasion of the United States by the Asian tiger mosquito in the 1980s) and agriculture, e.g. through loss of crops (Elton 1958; Holway *et al*. 1998), and may also affect the structure of ecosystems or the maintenance of native biological diversity (McKelvey 1975; Vitousek *et al*. 1996; Robinson 1996; Moller 1996). In particular, several Hymenoptera species have been introduced into many parts of the world and have now successfully colonized new territories (Moller 1996). Of the many invasive insect species, ants have received more attention because they are an important component of many terrestrial ecosystems (Morrison 2004), providing services such as pollination (Visser *et al*. 1996; Blancafort & Gómez 2005) and seed dispersal (Bond & Slingsby 1984). Ants are highly successful invaders of both islands and continents (McGlynn 1999) and like many invasive species, once they have invaded new areas, they can substantially alter the entire community (Christian 2001; O'Dowd *et al*. 2003; Lester 2005). A number of ant species are well known invaders in many parts of the world (Table 1), and of these, *Wasmannia auropunctata*, *Pheidole megacephala*, and *Anoplolepis gracilipes,* are far less studied (Lach 2003) and therefore more research is needed on these species and their impact on native biodiversity in the regions that they have invaded.

Most invasive ant species have similar characteristics – they are polygynous, unicolonial, they reproduce through budding of the nest (Sanders *et al*. 2001; Tsutsui & Suarez 2003),

they occur in close association with humans and are largely dispersed by humans unintentionally (Hölldobler & Wilson 1990; Wetterer *et al*. 1999). They can also become major household and agricultural pests, for example, *P. megacephala* in South Africa (although this species is indigenous to South Africa) (Prins *et al*. 1990) and Malaysia (Loke & Lee 2004). The major consequence associated with ant invasion is that they displace native ants in areas where they invade (Ward 1987, Holway 1999), and since ants are important partners in mutualistic relationships changes to native ant communities may cascade to other taxa and trophic levels (Bond & Slingsby 1984; Suarez *et al*. 1999; Tsutsui *et al*. 2001). Some animals, plants, and native arthropod fauna can also be directly or indirectly affected by this invasion, leading to reduction of their abundance (Cole *et al*. 1992; Oliveras *et al*. 2005). Impacts of invasive ant species on seed dispersal (Bond & Slingsby 1984; Christian 2001; Witt *et al*. 2004) and pollination (Blancafort & Gómez 2005) have also been reported. Furthermore, some ant species such as *Solenopsis invicta* and *Wasmannia auropunctata* excrete chemical compounds that are harmful to vertebrates (*sensu* Wetter *et al*. 1999), and humans.

Invasive ants often colonize disturbed areas and can also become an economic problem (Armbrecht & Ulloa-Chacón 2003). They occur in high population densities, which increases their potential for negative impacts on native invertebrates and vertebrate species, as well as communities (Allen *et al*. 2001). Invasive ants may also displace each other in areas where they both occur. For example in Florida, where the Argentine ant has been displaced by the red fire ant, *Solenopsis invicta* (Porter *et al*. 1988; also *sensu* Reimer 1994; Klotz *et al*. 1995). The Argentine ant (*Linepithema humile*) and *Pheidole megacephala*, both invasive species, also fail to coexist with each other (Hölldobler & Wilson 1990). Habitat preferences of these species bring them into direct competition with each other (Haskins & Haskins 1965).

The Argentine ant

The Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae) (previously *Iridomyrmex humilis*) is among the world's most successful invasive animal species (Lowe *et al*. 2000; Wild 2004). It is a native to Argentina, South America, and has become established in Mediterranean and subtropical climates throughout the world (Hölldobler & Wilson 1990; Tsutsui *et al*. 2001; Suarez *et al*. 2002). The Argentine ant is now a major pest in South Africa, Chile, Australia, United States, Britain, Belgium, Brazil, France, Bosnia, Italy, Germany and Spain (Haskins & Haskins 1965; McGlynn 1999; Vega & Rust 2001). Although the Argentine ant prefers Mediterranean and subtropical climates worldwide, it continues to

expand its range into new areas largely through human-mediated dispersal (Slingsby 1982; Passera 1994; Holway 1995; Sanders *et al*. 2001).

Throughout the world, the Argentine ant has been found to thrive in habitats with permanent sources of water, but decreases greatly in numbers with increasing distance into adjacent drier vegetation (Holway 2005). In the lower Sacramento Valley of California, Ward (1987) found the Argentine ant to be widely distributed and locally abundant in sites with permanent sources of water. Previous work also suggests that other environmental factors, especially temperature, are of great importance in the distribution of ant assemblages, including the Argentine ant (Human *et al*. 1998; Witt & Giliomee 1999; Holway *et al*. 2002a; Walters & Mackay 2004; Oliveras *et al*. 2005; Krushelnycky *et al*. 2005). Ants, in general, are most active in warm or hot temperatures, and the Argentine ant prefers low soil surface temperatures (15-19 °C) (Witt & Giliomee 1999).

Argentine ants are unicolonial throughout their introduced range, maintaining large supercolonies with very little or no intraspecific aggression (Suarez *et al*. 1999). These supercolonies have weak to non-existent behavioral boundaries, and queens and workers move freely among spatially separate nests (Markin 1970; Tsutsui *et al*. 2000). The colony size and foraging behavior of the Argentine ant may contribute to its success as an invader, and also in exploiting resources more quickly than other ant species (Human & Gordon 1996, 1997; Holway 1998a, 1998b, 1999; Walters & Mackay 2005). The aggressive foraging behaviour of workers, as well as the multiple queens per nest, also contribute to its success as an invader (Passera 1994). Argentine ant populations often abandon their nests when environmental conditions become unfavourable (Markin 1970; Vega & Rust 2001), and also when food becomes scarce (Holway & Case 2000). New nests are then reestablished when conditions become more favourable (Vega & Rust 2001). During nest relocation, queens and brood are vulnerable to predators as well as unexpected changes in the environment (Holway & Case 2000).

The major impact associated with the Argentine ant's invasion is the displacement of native ants in areas where it invades (Haskins & Haskins 1965; Ward 1987; De Kock 1990; Holway *et al*. 2002b), and it thus disrupts the structure of native ant communities (Carpintero *et al*. 2005). The species also affects the abundance and distribution of other arthropods (Cole *et al*. 1992), as well as some vertebrates. For example, Fisher *et al*. (2002) found that the abundance of the coastal horned lizard, an ant specialist, was severely reduced due to changes in the native ant community as a result of the Argentine ant invasion (Suarez *et al*. 2000; Holway *et al*. 2002b). Two mechanisms have been proposed to explain the displacement of the native ant fauna caused by the Argentine ant invasion: exploitative and interference

competition (Human & Gordon 1996; Holway 1999). During exploitative competition, Argentine ants discover and utilize bait faster than native ants; whereas in interference competition, they use their chemical compounds to fight and displace native ants (Holway 1999).

Several control strategies for the Argentine ant have been implemented, however, no strategy has proven entirely successful in controlling this species in agricultural, urban, or natural areas (Soeprono & Rust 2004). Very few attempts have been made to control the Argentine ant in natural areas (Costa & Rust 1998; Klotz *et al*. 2000; Rust *et al*. 2000; Costa *et al*. 2001; Klotz *et al*. 2002; Soeprono & Rust 2004). The most common approach used, and also the most effective, is baiting with various chemicals (Rust & Knight 1990; Klotz *et al*. 2000; *sensu* Klotz *et al*. 2002). Argentine ants occur in large colonies (Suarez *et al*. 1999), with nests of up to a square meter in size. Therefore, a bait must have an active ingredient with delayed toxicity and should be shared throughout the colony in order to kill all the workers, queens and larvae (Knight & Rust 1991; Hooper-Bui & Rust 2000; Klotz *et al*. 2002; Vega & Rust 2003). Finding the most suitable bait that will be consumed in large enough amounts is difficult (Soeprono & Rust 2004). Furthermore, baiting individual nests can be labour intensive, and often larger areas need to be treated to prevent re-infestations (Vega & Rust 2003). Markin (1970) found that foraging by Argentine ant workers was seasonal, and their selection of bait type, i.e. carbohydrates or proteins, may depend on the physiological and reproductive state of the colony (Rust *et al*. 2000). Understanding the seasonal life cycle of the Argentine ant is therefore an important step towards successful control of this species. Other challenges faced in the control of the Argentine ant include the killing of non-target organisms, high control costs (Vitousek *et al*. 1997), and threats to human health due to high pesticide usage in homes (Gordon *et al*. 2001). The most effective way to control the Argentine ant is therefore to prevent its introduction into new areas or to try and limit its spread from currently occupied areas.

The Argentine ant in South Africa

The Argentine ant was probably accidentally brought into Southern Africa in a fodder consignment during the Anglo-Boer war in the 1800s (Slingsby 1982; Witt 1993). Initially, it was known to be only associated with human-influenced landscapes (Carpintero *et al*. 2003; 2005), but it has been recorded in the undisturbed fynbos vegetation of the Western Cape Province of South Africa (Slingsby 1982; Bond & Slingsby 1984; Donnelly & Giliomee 1985; De Kock & Gilliomee 1989).

Ants play an important role in myrmecochory (the process of seed dispersal by ants), particularly in the Cape Floristic Region. Like other forms of animal seed dispersal, myrmecochory is viewed as a positive association in which ants increase the likelihood of successful reproduction of individual plants (myrmecochores) by spatially redistributing their seed (Whitney 2002). Foraging ants clasp the seed, usually by the elaiosome (food bodies attached externally to the seed), and carry it to their nests where the elaiosome is eaten and the seed discarded, either within the nest or on the surface litter (Bond & Slingsby 1983, 1984; Whitney 2002, Gómez & Oliveras 2003).

The Argentine ant is a poor seed disperser, and it often displaces native ants in its introduced range (Bond & Slingsby 1984; De Kock 1990; Suarez *et al*. 1998), particularly those indigenous species such as *Pheidole capensis* (Mayr), *Anoplolepis custodiens* (Smith), and *A. steingroeveri* (Forel) that are important seed dispersers of myrmecochorous seeds (Slingsby & Bond 1983; De Kock & Gilliomee 1989; Witt & Gilliomee 2004). However, Witt and Gilliomee (2005) found that the Argentine ant is capable of dispersing small seeds but not larger elaiosome-bearing seeds. After eating the elaiosome, the Argentine ant deposits the seeds above ground, making them vulnerable to desiccation, predation (Slingsby & Bond 1981; Bond & Breytenbach 1985) and fire (Bond & Stock 1989), and thus the seeds will have less chance of germinating (Christian 2001).

Fynbos flora has many endemic, myrmecochorous species, therefore the presence of the Argentine ant may become a major factor in the local extinction of some plant species (Slingsby & Bond 1981; De Kock & Giliomee 1989; Witt *et al*. 2004; Witt & Gilliomee 2004). Bond and Slingsby (1984) found lower probability of seedling emergence in invaded areas compared to uninvaded areas. Although many fynbos ant species are eliminated from invaded areas, other ant species, such as *Ocymyrmex cilliei* and *Tetramorium quadrispinosum* have the ability to coexist with the Argentine ant (Witt & Gilliomee 1999; Christian 2001).

Few studies have been conducted on the Argentine ant in South Africa, particularly in the Western Cape Province. Specific areas that have been studied include the impact of the Argentine ant on seed dispersal (Bond & Slingsby 1984; Christian 2001; Witt *et al*. 2004); its interaction with native ant species in fynbos vegetation (De Kock & Giliomee 1990; Christian 2001); its distribution in South African fynbos vegetation (De Kock & Giliomee 1989), as well as temperature range at which it is most active (Witt & Giliomee 1999). Most of these studies were conducted at Jonkershoek Nature Reserve and Kogelberg Biosphere Reserve. Helderberg Nature Reserve, however, has not previously been surveyed for the presence of this species, although it has recently been recorded there (Boonzaaier 2006). Apart from these

very few studies conducted, the detailed distribution of the Argentine ant inside these reserves is still not well known. Furthermore, its distribution in South Africa is poorly understood.

The prevalence of the Argentine ant in urban areas (houses and gardens), although assumed to be high, has also not been quantified. The spread of alien invasive pest species is one of the greatest threats to the long-term health and biological diversity of both urban and non-urban landscapes (Grewal *et al*. 2002). Like all tramp species, the Argentine ant lives in close association with humans (Passera 1994), and can therefore be easily transported into new areas through human activities (Vega & Rust 2001). It is therefore important to quantify the prevalence of the Argentine ant in urban areas, because these urban areas, if invaded, could potentially serve as sources of invasion into nearby natural vegetation and as stepping stones for further range expansion across South Africa (De Kock & Gilliomee 1989; Johnson 1992; Capintero *et al*. 2003; Lessard & Buddle 2005; Holway 2005).

Thesis aims and outline

The displacement of native ant species by the Argentine ant in its introduced ranges has been reported in many parts of the world, particularly in California (Ward 1987; Erickson 1971; Human & Gordon 1996; Holway & Suarez 2006). However, in South Africa, no studies have explicitly examined the impact of the Argentine ant on the local ant fauna, although some studies have made some observations in this regard (Christian 2001; De Kock 1990). Thus, in this study, the impact of the Argentine ant on the species diversity and composition of the local native ant fauna was assessed (reported in Chapter 2).

Second, the distribution of the Argentine ant inside three protected areas in the Western Cape Province was quantified (reported in Chapter 3). Microhabitat preferences influencing the distribution of this species within these areas were also determined. As shown elsewhere in the world, particularly in California, the distribution of the Argentine ant is often associated with soil moisture and free standing water availability, as well as areas with high anthropogenic disturbances (Ward 1987; Holway *et al*. 2002a; Carpintero *et al*. 2003; DiGirolamo & Fox 2006; Menke & Holway 2006).

Third, a countrywide survey was conducted to quantify the distributional extent of the Argentine ant in urban South Africa (reported in Chapter 4). In addition, this study assessed for possible expansion in the distribution range of the Argentine ant within the Western Cape Province since previous sampling by De Kock (1990) over 20 years ago.

The chapters in this thesis were written as individual manuscripts and there is thus some repetition in each. Finally, a general conclusion (Chapter 5) provides a brief summary of the

main findings of this study, and also discusses the implications of the Argentine ant invasion for system functioning. This study also provides some directions for future research with regard to the Argentine ant invasion.

REFERENCES

ALLEN, C.R., LUTZ, R.S., LOCKLEY, T., PHILLIPS, S.A. & DEMARAIS, S. 2001. The non-indigenous ant, *Solenopsis invicta*, reduces loggerhead shrikes and native insect abundance. *Journal of Urban Entomology* **18**: 249-259.

ARMBRECHT, I. & ULLOA-CHACÓN, P. 2003. The little fire ant *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae) as a diversity indicator of ants in tropical dry forest fragments of Colombia. *Environmental Entomology* **32**: 542-547.

BLANCAFORT, X. & GÓMEZ, C. 2005. Consequences of the Argentine ant, *Linepithema humile* (Mayr), invasion on pollination of *Euphorbia characias* (L.) (Euphorbiaceae). *Acta Oecologica* **28**: 49-55.

BOND, W.J. & SLINGSBY, P. 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *South African Journal of Science* **79**: 231-223.

BOND, W.J. & SLINGSBY, P. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorus Proteaceae. *Ecology* **65**: 1031-1037.

BOND, W.J. & BREYTENNACH, G.J. 1985. Ants, rodents and seed predation in Proteaceae. *South African Journal of Zoology* **20**:150-154.

BOND, W.J. & STOCK, W.D. 1989. The costs of leaving home: ants disperse myrmecochorus seeds to low nutrient sites. *Oecologia* **81**: 412-417.

CAMPBELL, D.J. & ATKINSON, I.A.E. 2002. Depression of tree recruitment by the pacific rat (*Rattus exulans* Peale) on the New Zealand's northern offshore islands. *Biological Conservation* **107**: 19-35.

CARPINTERO, S., REYES-LÓPEZ, J., & ARIAS DE REYNA, L. 2003. Impact of human dwellings on the distribution of the exotic Argentine ant: a case study in the Doñana National Park, Spain. *Biological Conservation* **115**: 279-289.

CARPINTERO, S., REYES-LÓPEZ, J., & ARIAS DE REYNA, L. 2005. Impact of Argentine ants (*Linepithema humile*) on an arboreal ant community in Doñana National Park, Spain. *Biodiversity and Conservation* **14**: 151-163.

CHRISTIAN, C.E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* **413**: 635-639.

COLE, F.R., MEDEIROS, A.C., LOOPE, L.L., & ZUEHLKE, W.W. 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology* **73**: 1313-1322.

COSTA, H.S & RUST, M.K. 1998. Mortality and foraging rates of Argentine ant (Hymenoptera: Formicidae) colonies exposed to potted plants treated with Fipronil. *Journal of Agricultural and Urban Entomology* **16**: 37-48.

COSTA, H.S., GREENBERG, L., KLOTZ, J. & RUST, M.K. 2001. Monitoring the effects of granular insecticides for Argentine ant control in nursery settings. *Journal of Agricultural and Urban Entomology* **18**: 13-22.

CUTHBERT, R. & HILTON, G. 2004. Introduced house mice *Mus musculus*: a significant predator of threatened and endemic birds on Gough Island, South Atlantic ocean? *Biological Conservation* **117**: 483-489.

DE KOCK, A.E. & GILIOMEE, J.H. 1989. A survey of the Argentine ant, *Iridomyrmex humilis* (Mayr), (Hymenoptera: Formicidae) in South African fynbos. *Journal of the Entomological Society of Southern Africa* **52**: 157-164.

DE KOCK, A.E. & GILIOMEE, J.H. 1990. Interactions between the introduced Argentine ant, *Iridomyrmex humilis* Mayr, and two indigenous fynbos ant species. *Journal of the Entomological Society of Southern Africa* **53**: 107-111.

DE KOCK, A.E. 1990. *The Argentine ant,* Iridomyrmex humilis *Mayr, indigenous ants and other epigaeic invertebrates of the fynbos in relation to fire and vegetation age*. MSc Thesis, University of Stellenboch, Stellenbosch.

DIGIROLAMO, L.A. & FOX, L.R. 2006. The influence of abiotic factors and temporal variation on local invasion patterns of the Argentine ant (*Linepithema humile*). *Biological Invasions* **8**: 125-135.

DONNELLY, D. & GILIOMEE, J.H. 1985. Community structure of epigaeic ants (Hymenoptera: Formicidae) in fynbos vegetation in the Jonkershoek valley. *Journal of the Entomological Society of Southern Africa* **48**: 247-257.

ELTON, C.S. 1958. *The ecology of invasions by animals and plants*. Methuen, London.

ERICKSON, J.M. 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. *Psyche* **78**: 257-266.

FAGAN, M.E. & PEART, D.R. 2004. Impact of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.) on juvenile recruitment by canopy trees. *Forest Ecology and Management* **194**: 95-107.

FISHER, R.N., SUAREZ, A.V. & CASE, T.J. 2002. Spatial patterns in the abundance of the coastal horned lizard. *Conservation Biology* **16**: 205-215.

FRENOT, Y., GLOAGUEN, J.C., MASSÉ, L. & LEBOUVIER, M. 2001. Human activities, ecosystem disturbance and plant invasions in subantarctic Crozet, Kerguelen, and Armsterdam Islands. *Biological Conservation* **101**: 33-50.

FRENOT, Y., CHOWN, S.L., WHINAM, J., SELKIRK, P.M., CONVEY, P., SKOTNICKI, M., BERGSTROM, D.M. 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Review* **80**: 45-72.

GORDON, D.M., MOSES, L., FALKOVITZ-HALPERN, M., & WONG, E.H. 2001. Effect of weather on infestation of buildings by the invasive Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). *American Midland Naturalist* **146**: 321-328.

GÓMEZ, C. & OLIVERAS, J. 2003. Can the Argentine ant (*Linepithema humile* Mayr) replace native ants in myrmecochory? *Acta Oecologica* **24**: 47-53.

GREMMEN, N.J.M., CHOWN, S.L. & MARSHALL, D.J. 1998. Impact of the introduced grass *Agrostis stolonifera* on vegetation and soil fauna communities at Marion Island, Sub-Antarctic. *Biological Conservation* **85**: 223-231.

GREWAL, P.S., GREWAL, S.K., MALIK, V.S. & KLEIN, M.G. 2002. Differences in susceptibility of introduced and native white grub species to entomopathogenic nematodes from various geographic localities. *Biological Control* **24**: 230-237.

GUREVITCH, J. & PADILLA, D.K. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* **19**: 470-474.

HAINES, I.H., HAINES, J.B. & CHERRETT, J.M. 1994. The impact and control of the crazy ant, *Anoplolepis longiceps* (Jerd.), in the Seychelles. In: Williams, D.F. (Ed). *Exotic ants*: *biology, impact and control of introduced species*. 206-218. Westview Press, Colorado, USA.

HASKINS, C.P. & HASKINS, E.F. 1965. *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda – equilibrium or slow replacement? *Ecology* **46**: 736-740.

HEE, J.J., HOLWAY, D.A., SUAREZ, A.V. & CASE, T.J. 2000. Role of propagule size in the success of incipient colonies of the invasive Argentine ant. *Conservation Biology* **14**: 559-563.

HÖLLDOBLER, B. & WILSON, E.O. 1990. *The ants*. Harvard University Press, Cambridge, Massachusetts.

HOLWAY, D.A. 1995. Distribution of the Argentine ant (*Linepithema humile*) in Northern California. *Conservation Biology* **9**: 1634-1637.

HOLWAY, D.A., SUAREZ, A.V. & CASE, T.J. 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science* **282**: 949-952.

HOLWAY, D.A. 1998a. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia* **116**: 252-258.

HOLWAY, D.A. 1998b. Factors governing rate of invasion: a natural experiment using Argentine ants. *Oecologia* **115**: 206-212.

HOLWAY, D.A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* **80**: 238-251.

HOLWAY, D.A. & CASE, T.J. 2000. Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant. *Animal Behaviour* **59**: 433-441.

HOLWAY, D.A., SUAREZ, A.V. & CASE, T.J. 2002a. Role of abiotic factors in governing susceptibility to invasion: A test with Argentine ants. *Ecology* **83**: 1610-1619.

HOLWAY, D.A., LACH, L., SUAREZ, A.V., TSUTSUI, N.D. & CASE, T.J. 2002b. The causes and consequences of ant invasions. *Annual Review of Ecological Systematics* **33**: 181-233.

HOLWAY, D.A. 2005. Edge effects of an invasive species across a natural ecological boundary. *Biological Conservation* **121**: 561-567.

HOLWAY, D.A. & SUAREZ, A.V. 2006. Homogenization of ant communities in Mediterranean California: the effects of urbanization and invasion. *Biological Conservation* **127**: 319-326.

HOOPER-BUI, L.M. & RUST, M.K. 2000. Oral toxicity of abamectin, boric acid, fipronil, and hydramethylnon to laboratory colonies of Argentine ants (Hymenoptera: Formicidae). *Journal of Economic Entomology* **93**: 858-864.

HUMAN, K.G. & GORDON, D.M. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* **105**: 405-412.

HUMAN, K.G. & GORDON, D.M. 1997. Effects of Argentine ants on invertebrate biodiversity in Northern California. *Conservation Biology* **11**: 1242-1248.

HUMAN, K.G., WEISS, S., WEISS, A., SANDLER, B. & GORDON, D.M. 1998. Effects of abiotic factors on the distribution and activity of the invasive Argentine ant (Hymenoptera: Formicidae). *Environmental Entomology* **27**: 822-833.

JOHNSON, S.D. 1992. Plant-animal relationships. In: Cowling, R.M. (Ed). *The ecology of fynbos*: *Nutrients, fire and diversity*. 175-205. Oxford University Press, Cape Town.

KENNEDY, T.A. 1998. Patterns of an invasion by Argentine ants (*Linepithema humile*) in a riparian corridor and its effects on ant diversity. *American Midland Naturalist* **140**: 343-350.

KLOTZ, J.H., MNGOLD, J.R., VAIL, K.M., DAVIS, L.R. & PATTERSON, R.S. 1995. A survey of the urban pest ants (Hymenoptera: Formicidae) of Peninsular Florida. *Florida Entomologist* **78**: 109-117.

KLOTZ, J., GREENBERG, L. & VENN, G. 2000. Evaluation of two hydramethylnon granular baits for control of Argentine ant (Hymenoptera: Formicidae). *Sociobiology* **36**: 201-207.

KLOTZ, J.H., RUST, M.K., COSTA, H.S., REIERSON, D.A. & KIDO, K. 2002. Strategies for controlling Argentine ants (Hymenoptera: Formicidae) with sprays and baits. *Journal of Agricultural and Urban Entomology* **19**: 85-94.

KNIGHT, R.L. & RUST, M.K. 1991. Efficacy of formulated baits for control of Argentine ant (Hymenoptera: Formicidae). *Journal of Economic Entomology* **84**: 510-514.

KNOWLER, D. & BABIER, E. 2005. Importing exotic plants and the risk of invasion: are market-based instruments adequate? *Ecological Economics* **52**: 341-354.

KOLAR, C.S. & LODGE, D.M. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* **16**: 199-204.

KRUSHELNYCKY, P.D., JOE, S.M., MEDEIROS, A.C., DAEHLER, C.C. & LOOPE, L.L. 2005. The role of abiotic conditions in shaping the long-term patterns of a high-elevation Argentine ant invasion. *Diversity and Distributions* **11**: 319-331.

LACH, L. 2003. Invasive ants: unwanted partners in ant-plant interactions? *Annals of the Missouri Botanical Garden* **90**: 91-108.

LAKE, J.C. & LEISHMAN, M.R. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom form herbivores. *Biological Conservation* **117**: 215-226.

LE BRETON, J., DELABIE, H.C., CHAZEAU, J., DEJEAN, A. & JOURDAN, H. 2004. Experimental evidence of large-scale unicoloniality in the tramp ant *Wasmannia auropunctata* (Roger). *Journal of Insect Behavior* **17**: 263-271.

LEE, C.E. 2002. Evolutionary genetics of invasive species. *Trends in Ecology and Evolution* **17**: 386-391.

LEE, K.A. & KLASING, K.C. 2004. A role for immunology in invasion biology. *Trends in Ecology and Evolution* **19**: 523-529.

LENZ, L. & TAYLOR, J.A. 2001. The influence of an invasive tree species (*Myrica faya*) on the abundance of an alien insect (*Sophonia rufofascia*) in Hawai'I Volcanoes National Park. *Biological Conservation* **102**: 301-307.

LESSARD, J.P. & BUDDLE, C.M. 2005. The effects of urbanization on ant assemblages (Hymenoptera: Formicidae) associated with the Molson Nature Reserve, Quebec. *Canadian Entomologist* **137**: 215-225.

LESTER, P.J. 2005. Determinants for the successful establishment of exotic ants in New Zealand. *Diversity and Distributions* **11**: 279-288.

LINDENMAYER, D.B. & MCCARTHY, M.A. 2001. The spatial distribution of non-native plant invaders in a pine-eucalypt landscape mosaic in South-eastern Australia. *Biological Conservation* **102**: 77-87.

LOKE, P.Y. & LEE, C.Y. 2004. Foraging behavior of field populations of the big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). *Sociobiology* **43**: 211-219.

LOWE, S., BROWNE, M., BOUDJELAS, S. & DE POORTER, M. 2000. 100 of the world's worst invasive alien: a selection from the Global Invasive Species Database. *The Invasive Species Specialist Group (ISSG), World Conservation Union (IUCN).*

MACK, M.C. & D'ANTONIO, C.M. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* **13**: 195-198.

MACK, R.N. & LONSDALE, W.M. 2001. Humans as global plant dispersers: getting more than we bargained for. *Bioscience* **51**: 95-102.

MAKI, K. & GALATOWITSCH, S. 2004. Movement of invasive aquatic plants into Minnesota (USA) through horticultural trade. *Biological Conservation* **118**: 389-396.

MARGOLIS, M., SHOGREN, J.F. & FISCHER, C. 2005. How trade politics affect invasive species control. *Ecological Economics* **52**: 305-313.

MARKIN, G.P. 1970. The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae), in Southern California. *Annals of the Entomological Society of America* **63**: 1238-1242.

MCGLYNN, T.P. 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography* **25**: 535-548.

MCKELVEY, J.J. 1975. Insects and human welfare. In: Pimentel, D. (Ed). *Insects, science and society*. Academic Press Inc. New York.

MENKE, S.B. & HOLWAY, D.A. 2006. Abiotic factors control invasion by Argentine ants st the community scale. *Journal of Animal Ecology* **75**: 368-376.

MOLLER, H. 1996. Lessons for invasion theory from social insects. *Biological Conservation* **78**: 125-142.

MORRISON, L.W. 2000. Mechanisms of interspecific competition among an invasive and two native fire ants. *Oikos* **90**: 238-252.

MORRISON, L.W. 2004. Spatiotemporal variation in antlion (Neuroptera: Myrmeleontidae) density and impacts on ant (Hymenoptera: Formicidae) and generalized arthropod foraging. *Annals of the Entomological Society of America* **97**: 913-922.

O'DOWD, D.J., GREEN, P.T. & LAKE, P.S. 2003. Invasional 'meltdown' on an oceanic island. *Ecology Letters* **6**: 812-817.

OLIVERAS, J., BAS, J.M., CASELLAS, D. & GÓMEZ, C. 2005. Numerical dominance of the Argentine ant vs native ants and consequences on soil resources searching in Mediteranean cork-oak forests (Hymenoptera: Formicidae). *Sociobiology* **45**: 643-658.

PASSERA, L. 1994. Characteristics of tramp species. In: Williams, D.F. (Ed). *Exotic ants*: *biology, impact and control of introduced species*. 23-43. Westview Press, Colorado, USA.

PIMENTEL, D., MCNAIR, S., JANECKA, J., WIGHTMAN, J., SIMMONDS, C., O'CONNEL, C., WONG, E., RUSSEL, L., ZERN, J., AQUINO, T. & TSOMONDO, T. 2001. Economic and environmental threats of alien plant, animal and microbe invasions. *Agriculture, Ecosystems and Environment* **84**: 1-20.

PORTER, S.D., VAN EIMEREN, B. & GILBERT, L.E. 1988. Invasion of red imported fire ants (Hymenoptera: Formicidae): microgeography of competitive replacement. *Annals of the Entomological Society of America* **81**: 913-918.

PORTER, S.D. & SAVIGNANO, D.A. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* **71**: 2095-2106.

PRINS, A.J., ROBERTSON, H.G. & PRINS, A. 1990. Pest ants in urban and agricultural areas of Southern Africa. In: Vander Meer, R.K., Jaffe, K, & Cedeno, A. (Eds). *Applied myrmecology*: *a world perspective*. 25-33. Westview Press, Colorado, USA.

REIMER, N.J. 1994. Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. In: Williams, D.F. (Ed). *Exotic ants: biology, impact and control of introduced species*. 11-22. Westview Press, Colorado, USA.

REJMÁNEK, M. 1996. A theory of seed plant invasiveness: the first sketch. *Biological Conservation* **78**: 171-181.

ROBINSON, W.H. 1996. *Urban entomology*: *insect and mite pests in the human environment*. Chapman and Hall, London.

RODRíGUEZ, C., TORRES, R. & DRUMMOND, H. In press. Eradicating introduced mammals from a forested tropical island. *Biological Conservation*.

ROSE, S. & FAIRWEATHER, P.G. 1997. Changes in floristic composition of urban bushland invaded by *Pittosporum undulatum* in Northern Sydney, Australia. *Australian Journal of Botany* **45**: 123-149.

RUST, M.K. & KNIGHT, R.L. 1990. Controlling Argentine ants in urban situations. In: Vander Meer, R.K., Jaffe, K. & Cedeno, A. (Eds.) *Applied myrmecology*: *a world perspective*. 663-670. Westview Press, Boulder, Colorado, USA.

RUST, M.K., REIERSON, D.A., PAINE, E. & BLUM, L. 2000. Seasonal activity and bait preferences of the Argentine ant (Hymenoptera: Formicidae). *Journal of Agricultural and Urban Entomology* **17**: 201-212.

SAMWAYS, M.J. 1996. Insects on the brink of a major discontinuity. *Biodiversity and Conservation* **5**: 1047-1058.

SAMWAYS, M.J, CALDWELL, P.M. & OSBORN, R. 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agriculture, Ecosystems and Environment* **59**: 19-32.

SANDERS, N.J., BARTON, K.E. & GORDON, D.M. 2001. Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. *Oecologia* **127**: 123-130.

SLINGSBY, P. 1982. The Argentine ant – how much of a threat? *Veld and Flora* **68**: 102-104.

SLINGSBY, P. & BOND, W. 1981. Ants – friends of the fynbos. *Veld and Flora* **67**: 39-45.

SLINGSBY, P. & BOND, W. 1983. Of ants and Proteas. *African Wildlife* **36**: 104-107.

STANDISH, R.J. 2004. Impact of an invasive clonal herb on epigaeic invertebrates in forest remnants in New Zealand. *Biological Conservation* **116**: 49-58.

STOUT, J.C., KELLS, A.R. & GOULSON, D. 2002. Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. *Biological Conservation* **106**: 425-434.

SOEPRONO, A.M. & RUST, M.K. 2004. Strategies for controlling Argentine ants (Hymenoptera: Formicidae). *Sociobiology* **44**: 669-682.

SUAREZ, A.V., BOLGER, D.T. & CASE, T.J. 1998. Effects of fragmentation and invasion on native ant communities in coastal Southern California. *Ecology* **79**: 2041-2056.

SUAREZ, A.V., TSUTSUI, N.D., HOLWAY, D.A. & CASE, T.J. 1999. Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. *Biological Invasions* **1**: 43-53.

SUAREZ, A.V., RICHMOND, J.Q. & CASE, T.J. 2000. Prey selection in horned lizards following the invasion of Argentine ants in Southern California. *Ecological Applications* **10**: 711-725.

SUAREZ, A.V., HOLWAY, D.A., LIANG, D., TSUTSUI, N.D. & CASE, T.J. 2002. Spatiotemporal patterns of intraspecific aggression in the invasive Argentine ant. *Animal Behaviour* **64**: 697-708.

TSUTSUI, N.D., SUAREZ, A.V., HOLWAY, D.A. & CASE, T.J. 2000. Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Science* **97**: 5948-5953.

TSUTSUI, N.D., SUAREZ, A.V., HOLWAY, D.A. & CASE, T.J. 2001. Relationships among native and introduced populations of the Argentine ant (*Linepithema humile*) and the source of introduced populations. *Molecular Ecology* **10**: 2125-2161.

TSUTSUI, N.D. & SUAREZ, A.V. 2003. The colony structure and population biology of invasive species. *Conservation Biology* **17**: 48-58.

VEGA, S.Y. & RUST, M.K. 2001. The Argentine ant – a significant invasive species in agricultural, urban and natural environments. *Sociobiology* **37**: 3-25.

VEGA, S.Y. & RUST, M.K. 2003. Determining the foraging range and origin of resurgence after treatment of Argentine ant (Hymenoptera: Formicidae) in urban areas. *Journal of Economic Entomology* **96**: 844-849.

VISSER, D., WRIGHT, M.G. & GILLIOMEE, J.H. 1996. The effect of the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), on flower-visiting insects of *Protea nitida* Mill (Proteaceae). *African Entomology* **4**: 285-287.

VITOUSEK, P.M., D'ANTONIO, C.M., LOOPE, L.L. & WESTBROOKS, R. 1996. Biological invasions as global environmental change. *American Scientist* **84**: 468-478.

VITOUSEK, P.M., D'ANTONIO, C.M., LOOPE, L.L., REJMÁNEK, M. & WESTBROOKS, R. 1997. Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* **27**: 1-16.

VON AESCH, L. & CHERIX, D. 2005. Introduced ant species and mechanisms of competition on Floreana Island (Galápagos, Ecuador). *Sociobiology* **45**: 1-19.

WALCK, J.L., BASKIN, J.M. & BASKIN, C.C. 1999. Effects of competition from introduced plants on establishment, survival, growth and reproduction of the rare plant *Solidago shortii* (Asteraceae). *Biological Conservation* **88**: 213-219.

WALTERS, A.C. & MACKAY, D.A. 2005. Importance of large colony size for successful invasion by Argentine ants (Hymenoptera: Formicidae): Evidence for biotic resistance by native ants. *Austral Ecology* **30**: 395-406.

WARD, P.S. 1987. Distribution of the introduced Argentine ant (Iridomyrmex *humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. *Hilgardia* **55**: 1-16.

WARD, D.F., HARRIS, R.J. & STANLEY, M.C. 2005. Human-mediated range expansion of Argentine ants *Linepithema humile* (Hymenoptera: Formicidae) in New Zealand. *Sociobiology* **45**: 401-408.

WETTERER, J.K., WALSH, P.D. & WHITE, L.J.T. 1999. *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae), a destructive tramp-ant, in wildlife refuges of Gabon. *African Entomology* **7**: 292-294.

WHITNEY, K.D. 2002. Dispersal for distance? *Acacia ligulata* seeds and meat ants *Iridomyrmex viridiaeneus*. *Austral Ecology* **27**: 589-595.

WILCOVE, D.S., ROTHSTEIN, D., DUBOW, J., PHILLIPS, A. & LOSOS, E. 1998. Quantifying threats to imperilled species in the United States. *Bioscience* **48**: 607-615.

WILD, A.L. 2004. Taxonomy and distribution of the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* **97**: 1204-1215.

WITT, A.B.R. 1993. *Factors affecting myrmecochory in fynbos*. MSc Thesis, University of Stellenbosch, Stellenbosch.

WITT, A.B.R. & GILLIOMEE, J.H. 1999. Soil-surface temperatures at which six species of ants (Hymenoptera: Formicidae) are active. *African Entomology* **7**: 161-164.

WITT, A.B.R., GEERTSEMA, H. & GILIOMEE, J.H. 2004. The impact of an invasive ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), on the dispersal of the elaiosome-bearing seeds of six plant species. *African Entomology* **12**: 223-230.

WITT, A.B.R. & GILLIOMEE, J.H. 2004. The impact of an invasive ant, *Linepithema humile* (Mayr), on the dispersal of *Phylica pubescens* Aiton seeds in South Africa. *African Entomology* **12**: 179-185.

Table 1. Five most important invasive ant species globally

Common name	Scientific name	Origin/native habitat	Current distribution	Selected references
Argentine ant	*Linepithema humile* Mayr	South America	Mediterranean and subtropical climates around the world	Suarez *et al*. 2002; Tsutsui *et al*. 2001
Red fire ant	*Solenopsis invicta* Buren	South America	Southeastern United States	Allen *et al*. 2001; Porter & Savignano 1990
Little fire ant	*Wasmannia auropunctata* Roger	Neotropical region	South and Central America and the Caribbean	Wetterer *et al*. 1999; Le Breton *et al*. 2004
Long-legged ant	*Anoplolepis gracilipes* F. Smith	Not well known	Tropics	Haines *et al*. 1994; O'Dowd *et al*. 2003
Big-headed ant	*Pheidole megacephala* Mayr.	Tropical Africa	Almost all subtropical habitats around the world	Passera 1994; Prins *et al*. 1990

CHAPTER 2

Impact of the Argentine ant on bait-visiting native ant fauna

INTRODUCTION

The Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), is considered one of the world's most ecologically devastating invasive species, and has been introduced to many parts of the world through human trade and commerce (Lowe *et al*. 2000). It is native to Argentina, South America, and its current distribution includes almost all areas with Mediterranean or subtropical climates worldwide (Hölldobler & Wilson 1990; Holway 1995). The Argentine ant is a typical tramp ant, (it prefers areas with high disturbances and lives in close association with humans (Passera 1994)), making it a significant pest in urban and agricultural areas on most continents (Ward 1987; Markin 1970; Prins *et al*. 1990).

Throughout its introduced range, the Argentine ant is largely associated with the displacement of native ant fauna in the areas where it invades (Erickson 1971; Ward 1987; Human & Gordon 1996; Holway 1999). In the Sacramento Valley, California, Ward (1987) found that the native ant fauna had been reduced by half at sites invaded by the Argentine ant. Most species are vulnerable to this displacement, particularly those involved in important ecosystem processes, such as seed dispersal and mutualistic interactions. For example, in San Diego County, California, Carney and colleagues (2003) found that seed dispersal was significantly lower in areas occupied by the Argentine ant compared to areas dominated by the indigenous *Pogonomyrmex subnitidus* (a seed dispersing ant). Similarly, in South Africa, Bond and Slingsby (1984) and Christian (2001) found lower seed dispersal and seedling emergence in areas invaded by the Argentine ant. This is due, in part, to the fact that the Argentine ant is a generalist feeder, and occurs in a wide range of habitats, thus directly interacting with many ant species (Majer 1994).

In addition to the direct impact of the Argentine ant on biodiversity, the species also has direct and indirect impacts on other taxa (Suarez *et al*. 2000). For example, the horned lizard (*Phrynosoma coronatum*), which is an ant-feeding specialist, is declining

throughout most of its range in California, USA, due to the negative impact of the Argentine ant on the native ant community (Suarez & Case 2002; Fisher *et al*. 2002). Furthermore, important ecosystem processes such as pollination may also be disrupted as an indirect effect of Argentine ant invasion (Blancafort & Gómez 2005), and the displacement of essential pollinators can threaten insect-pollinated plants, as has been shown in Hawaii (Cole *et al*. 1992). In the Western Cape Province of South Africa, the Argentine ant has been associated with outbreaks of the red scale insect (*Aonidiella aurantii*) (Samways *et al*. 1982) and the mealybug (*Planococcus ficus*) in orchards and vineyards respectively (Addison & Samways 2000). Elsewhere in the world, the Argentine ant has reportedly caused nest failure in bird chicks through predation (Suarez *et al*. 2005). However, this effect is not well studied.

In understanding the dynamics of the Argentine ant invasion, there are three types of interactions between the Argentine ant and native ant species that are of primary interest: (1) the direct negative impact of the Argentine ant on native ant species, e.g. via competition and predation (Human & Gordon 1996); (2) neutral interactions involving those native species that are able to coexist with the Argentine ant (Christian 2001), and (3) native ant species that outcompete or are able to resist invasion by the Argentine ant (Ward 1987), i.e. biotic resistance. The biotic resistance hypothesis, proposed by Elton (1958), predicts that areas with high species richness will be less likely to experience biological invasion than areas with lower species richness. Evidence of biotic resistance in ant communities have been demonstrated by Ward (1987) and Walters and Mackay (2005).

Two mechanisms contribute to the competitive nature of the Argentine ant, i.e. exploitative and interference competition (Hölldobler & Wilson 1990; Human & Gordon 1996). During exploitative competition, Argentine ants often locate and utilize food sources more quickly than their native counterparts (Human & Gordon 1996; Holway 1998a). Thus, the Argentine ant affects native ants indirectly by utilizing the available food before native ants can get to it. However, it is also theoretically possible that some native ants may benefit from this exploitation. For example, if species A, which shares the same resources with species B, is displaced, then species B has more resources available to it. Therefore, the Argentine ant has a positive indirect effect (known as

indirect facilitation, *sensu* White *et al*. 2006) on species B, although this is only possible if species B can coexist with the Argentine ant. This form of interaction between the Argentine ant and native ants has not been documented (White *et al*. 2006).

Interference competition occurs when the Argentine ant interferes with activities and foraging behaviour of native ant species, often by preying on them (Human & Gordon 1996; Cerdá *et al*. 1998). Argentine ants often form very large colonies, with thousands of workers and multiple queens in one nest (Tsutsui & Suarez 2003; Holway & Suarez 2004; Walters & MacKay, 2005). In contrast, most native ant species have small colonies compared to that of the Argentine ant and often contain only one queen per nest (Hölldobler & Wilson 1990). Argentine ants are therefore often able to reproduce, spread and occupy large areas at a much higher rate than their native counterparts (Human & Gordon 1996; Holway 1998b). Like most invasive ant species, the introduced populations of the Argentine ant lack territorial boundaries and intraspecific competition (Porter & Savignano 1990). Nest raiding, although not well documented, is another form of interference competition used by Argentine ants to displace native ants (Holway *et al*. 2002). For example, in coastal southern Carlifornia, Zee and Holway (2006) found that Argentine ants often raid nests of the harvester ant, *Pogonomyrmex subnitidus*. Niche preferences, i.e. nesting sites, time of foraging and food availability and quality, may also play a role in shaping ant populations within an area, and the greater the difference in preference between species, the greater the chance that the dynamics of the two species populations will be independent of each other (Hölldobler & Wilson 1990). Thus, native ant species with similar or identical niche preferences to that of the Argentine ant are most vulnerable to displacement.

Although the Argentine ant displaces many indigenous ant species, there are some species that are able to coexist with it. For example, in South Africa two species, *Tetramorium quadrispinosum* and *Meranoplus peringueyi* have been found together (in the same pitfall traps) with the Argentine ant (Christian 2001; Addison & Samways 2000). This co-occurrence may be explained by differences in the species' foraging habits and foraging times, i.e. epigaeic versus arboreal and diurnal versus nocturnal, and also their respective functional groups. In Australia, Walters (2006) collected three native ant genera in greater densities at invaded sites. This was due to the foraging habits of

these genera (two genera were cryptic and one solitary) that allows them to avoid interaction with the Argentine ant, an epigaeic forager. The Argentine ant belongs to the Dominant Dolichoderinae functional group (*sensu* Andersen 1997a, 2000; Hoffmann & Andersen 2003, for characteristics of different functional groups). Around the globe, species belonging to the functional groups Specialist Predators (e.g. genus *Pachycondyla*) and Cold Climate Specialist (e.g. genus *Leptothorax*) are generally considered to avoid interaction with the Argentine ant (Andersen 1997a). However those species belonging to the Subordinate Camponotini, (e.g. genus *Camponotus*) and Opportunists functional groups, (e.g. genus *Tetramorium*) often coexist with the Argentine ant (Hoffmann & Andersen 2003).

Despite its highly competitive nature, some studies have reported the displacement of the Argentine ant by other ant species. For example, Reimer (1994) reported that the Argentine ant was displaced by *Pheidole megacephala* (a species native to central Africa (Haskins & Haskins 1988)) in the Hawaiian Islands (also *sensu* Fluker & Beardsley 1970). To date, very few studies have reported this type of displacement. Some previous studies, however, have reported the displacement of *P. megacephala* by the Argentine ant (Haskins & Haskins 1965, 1988; Crowell 1968). This type of displacement is also influenced by climate, i.e. the Argentine ant displaces *P. megacephala* in temperate areas, whereas *P. megacephala* displaces the Argentine ant in tropical areas. Native ant species may also resist invasion by the Argentine ant, particularly at range edges, and thus limiting its spread into other areas through biotic resistance (Elton 1958; Walters & MacKay 2005). A laboratory experiment conducted by Walters and MacKay (2005) between the Argentine ant and *Iridomyrmex rufoniger* (an Australian native ant species) showed that *I. rufoniger* may reduce the spread of the Argentine ant, particularly if *I. rufoniger* has higher abundance than the Argentine ant. However, few studies have examined this type of interaction between the Argentine ant and native ants in the natural environment in South Africa and elsewhere in the world.

South Africa is one of the countries successfully invaded by the Argentine ant. Although the impacts of this species on South African biodiversity are generally poorly understood, the consequences of the Argentine ant' invasion on seed dispersal have been studied in some protected areas of the WCP (Witt 1993; Bond & Slingsby 1984;

Christian 2001; Witt *et al*. 2004). The Argentine ant has been shown to displace important native ant species such as *Anoplolepis custodiens* and *Pheidole capensis* involved in seed dispersal in South African Fynbos vegetation (Christian 2001). Native ants are attracted to the elaiosome (the fleshy part of the seed), and often bury the seeds after eating the elaiosome (Bond & Slingsby 1983). The Argentine ant, however, does not bury the seed, and this makes the seed vulnerable to desiccation, predation (Slingsby & Bond 1981; Bond & Breytenbach 1985) and fire (Bond & Stock 1989). Therefore, myrmecochorous plants (plants that rely on ants for seed dispersal) are vulnerable to the invasion by the Argentine ant, and may have lower germination rates (Bond & Slingsby 1984). In Kogelberg Biosphere Reserve, Bond and Slingsby (1984) found that there was lower seed dispersal and seedling emergence in areas invaded by the Argentine ant compared with uninvaded areas, while Witt (1993) found a similar pattern at Jonkershoek Nature Reserve, where larger seeds were particularly vulnerable to a decline in dispersal rate as a consequence of invasion by the Argentine ant.

Although it has been shown that the Argentine ant has invaded protected areas in South Africa, and that it affects seed dispersal inside these protected areas (Bond & Slingsby 1984; Witt 1993), no studies have explicitly tested the displacement of native ant species by the Argentine ant in the Cape Floristic Region, although Christian (2001) and De Kock (1990) made some observation in this regard. The form of the relationship between the Argentine ant and individual species in native ant assemblages has also not been examined. Thus, limited information is available, from few sites, on which native ant species are negatively affected by the presence of the Argentine ant and which are unaffected, and how this varies between habitat types. Identifying those species that are negatively affected will contribute to understanding the functional consequences of invasion by the Argentine ant. Therefore, in this study the impact of the Argentine ant on the species diversity and composition of bait-visiting native ant fauna was assessed in three protected areas in the Boland Region of the Western Cape Province, South Africa. The impact of this species was also assessed at five microhabitas, i.e. buildings, lawn, roadside, vegetation and waterbodies. Four microhabitats were sampled at Jonkershoek Nature Reserve, and five at Helderberg and Kogelberg Biosphere Reserves (see Table 1 for number of bait stations placed at each microhabitat). In addition, species associations

and the covariation in species abundances were compared between invaded and uninvaded areas.

MATERIALS AND METHOD

Study sites

This study was conducted in three protected areas in the Boland region of the south Western Cape Province, South Africa (i.e. Jonkershoek Nature Reserve (JNR), Helderberg Nature Reserve (HNR) and Kogelberg Biosphere Reserve (KBR)). The southern part of the Western Cape Province has a Mediterranean-type climate, with winter rainfall (June-August) and a warm, dry summer (October-March). The reserves in the study are dominated by Fynbos vegetation, i.e. an evergreen, narrow-leaved sclerophyllous shrubland growing on young, shallow, nutrient poor soils (Witch *et al*. 1969; Moll & Jarman 1984; Schlettwein & Giliomee 1987; Cowling & Holmes 1992). In addition, these protected areas contain other habitat types: mountain, riparian, forest and lowland vegetation (Boucher 1978; Le Maitre *et al*. 1996). Each reserve encompasses perennial streams supporting a continuous river stretching across the reserve (Fig. 3, Chapter 3). The protected areas also include recreational areas, such as picnic sites and hiking trails, and they attract a large number of people on a daily basis, especially during the summer period.

Helderberg Nature Reserve (34°03' S, 18°52'E) is situated outside the town of Somerset West, and is dominated by Mesic Mountain Fynbos (Http://www.helderbergnaturereserve.co.za), as well as patches of Renosterveld vegetation (Van Wyk & Smith 2001). At 385 hectares, HNR is the smallest of the three protected areas in this study, and information on climate and soil of this nature reserve is limited. However, the climate is likely to be very similar to Jonkershoek Nature Reserve.

Jonkershoek Nature Reserve (34°58' S, 18°56'E) is situated approximately 15 km south-east of Stellenbosch, and covers an area of 9 800 hectares. In addition to the Fynbos vegetation (Van Wyk & Smith 2001) inside the reserve, there is a large pine plantation neighboring, although not officially part of, this nature reserve. The mean

annual rainfall of the area is approximately 1600 mm, and temperatures fluctuate between approximately 1°C and 39°C, with a mean monthly maximum temperature of approximately 23°C in January and a mean monthly minimum of approximately 8°C in July (De Kock 1990).

Kogelberg Biosphere Reserve (34°19' S, 18°58'E) is situated approximately 90 km south-east of Cape Town and covers a total area of 20 000 ha. The reserve has an average annual rainfall of 1000-1500 mm (Van Wilgen & Richardson 1985; Johns & Johns 2001), and temperatures vary between 2 °C and 35 °C (Boucher 1978). The vegetation includes undisturbed Fynbos communities, and also areas of old cultivation and pine and eucalypt windbelts (Bond & Slingsby 1984).

Sampling

Sampling was done between February and April 2005, October and November 2005 and January and February 2006 (peak activity period for most ant species (Johnson 1992)). Sampling was discontinued on days on which air temperature reached 30 °C before 1 pm, as the Argentine ant activity started declining when temperatures exceeded 30 °C (N.M. Luruli, personal observation). The optimal temperature range for the Argentine ant is 15°C – 30 °C (Witt & Giliomee 1999; Thomas & Holway 2005). Each reserve was divided into grid cells of the same size using 1: 50 000 topographic maps (obtained from Surveys and Mapping, Mowbray, Cape Town, South Africa). Grid cells were created in Arcview version 3.2 with latitude and longitude intervals of 25 seconds (i.e. quarter-degree/minute grid cells at ca. 0.17 km^2). However, Kogelberg Biosphere Reserve, which is the largest of the three reserves, was for logistic reasons, sampled using two different grid sizes. First, a larger grid with one minute intervals (ca. 2.8 km^2) was used to cover the entire nature reserve, and thereafter smaller (25 seconds interval) grid cells were used. All accessible cells of the largest grid size were surveyed for the Argentine ant. For each grid cell, five bait stations were placed as close to the center of the grid as possible. In cases where the center of the grid was inaccessible (due to physical constraints such as thick vegetation or a mountainous area), bait stations were placed at the most accessible point closest to the center of the grid cell. To ensure that each sample was independent of

the other, a minimum distance of 10 m between bait stations was maintained (Human & Gordon 1996; Holway 1998a, b; Andersen *et al*. 2002; Parr *et al*. 2004; Netshilaphala *et al*. 2005; Botes *et al*. 2006).

Bait station trapping

During February 2005, a pilot study was conducted at J.S. Marais Nature Reserve, Stellenbosch (33°93' S, 18°87' E). This is a very small reserve (approximately 25 ha), which includes Fynbos vegetation and patches of old pine and eucalyptus trees. The aim of this pilot study was to test different types of baits to determine the most effective bait for attracting the Argentine ant. Four protein-based bait types, i.e. tuna fish, cubes of unprocessed beef, tuna-flavoured and beef-flavoured catfood, were tested. Previous studies have shown that protein-based baits effectively attract the Argentine ant (Witt 1993; Holway 1998a; Thomas & Holway 2005)

Three replicates of each bait type were randomly placed in three transects, forming a grid (i.e. a total of 12 individual bait stations). Baits were placed 10 m apart and were left open for one hour, after which they were collected, placed in containers with 100 % ethanol and taken back to the laboratory. The contents of all the bait types were examined under a microscope, and ant species were identified in most cases to species level. The mean (± S.E.) number of Argentine ants collected at tuna fish baits was 38.33 ± 0.52, whereas 5.0 ± 1.44, 0.33 ± 5.59 and 5.67 ± 1.35 were collected at beef cubes, tuna-flavoured and beef-flavoured catfood respectively. Tuna fish was thus considered the most effective bait type, and was therefore chosen as the bait for the main study.

The canned tuna fish in oil (approximately one teaspoon) that was used as bait was placed on white, 90 mm diameter round filter paper to aid collection of the bait after 1 h exposure. This baiting method is commonly used when estimating the species richness and composition of epigaeic ant fauna, as well as to examine the activities and behavior of ants (Bestelmeyer *et al*. 2000). This method is also a very useful tool for comparing ant species in terms of different components of competitive ability and can provide information on habitat use (Hölldobler & Wilson 1990; Bestelmeyer 1997)). However, this method does have some disadvantages. It is difficult to standardize when using it to

compare invertebrate abundances between sites (Sutherland 1996). Also, not all ant species are attracted to the type of bait used and several species will not be sampled with this method (Sutherland 1996). Although the species attracted to the bait are most likely to be generalists, these generalists do represent a large proportion of ant faunas around the world and may be used to examine some patterns in ant communities (Bestelmeyer *et al*. 2000). Comparisons across this subset of local ant fauna are also valid. They are also likely to include the native ant species that would compete most directly with the Argentine ant for food resources. Argentine ant workers are epigaeic (they forage above ground) and they interact with many epigaeic native ant species, often leading to the exclusion of native ants by the Argentine ant (Human & Gordon 1996). Several similar studies conducted elsewhere in the world have used this baiting method to assess the interaction and competition between the Argentine ant and native epigaeic ant fauna (Ward 1987; Human & Gordon 1996, 1999; Holway 1998a, 1999; Thomas & Holway 2005). In this study, bait stations were thus used to indirectly assess the impact and interaction between the Argentine ant and generalist native ant species attracted to the same bait.

Baits were covered with wire mesh cages (30 x 15 cm diameter in size, with 5 mm diameter openings in mesh) to exclude larger scavengers (such as rodents, lizard and birds) from the bait. These cages had 2 cm long wires extended at the bottom for stabilizing them in the ground. At each bait station, a red and white plastic marker was tied around nearby vegetation to facilitate relocation of the bait. After one hour, all the ants feeding at the bait station were collected, placed in containers with 100 % ethanol and taken back to the laboratory where they were identified under a microscope. Ant species were identified, in most cases to genus level and in some cases to species level (identifications confirmed by Dr. A. Botes, University of Stellenbosch). Voucher specimens are kept at the DST-NRF Center for Invasion Biology, University of Stellenbosch, South Africa.

Data analyses

Ant species richness

Rarefaction curves were compiled for each protected area to estimate sampling representivity (Gotelli & Colwell 2001). Generalized Linear Models (GLZ), assuming a Poisson error distribution (log link function, Type 3 model, Dobson 2002) were used to compare species richness between invaded and uninvaded bait stations at all three protected areas, using the factors : (1) bait station status (invaded or uninvaded) and (2) protected area (HNR, JNR and KBR). Mean number of ant species in different microhabitats was also compared using GLZ. Because protected areas did not all have the same microhabitats, each protected area was analyzed separately in this case. Two microhabitats (building and lawn) that were occupied only by the Argentine ant at HNR were excluded from the analysis.

Ant species abundance and occupancy

To assess the impact of the Argentine ant abundance on the abundances of native ants, the abundance of each native ant species was compared between invaded and uninvaded bait stations at each nature reserve. Even though ant abundance data are biased by the fact that the species are social, and by the relative position of the bait to the closest nests, abundance data do provide valid estimates of relative local dominance by species (Holway 1998a; Human & Gordon 1999). Abundances of each species were compared between invaded and uninvaded bait stations using relative abundance distributions. To test whether the Argentine ant abundance had a significant impact on native ant abundances, Generalized Linear Models, assuming a Poisson error distribution (log link function, Type 3 model, Dobson 2002) were used to test for significant differences in species abundances between invaded and uninvaded bait stations, using the variables (1) species abundance and (2) the Argentine ant status (invaded or uninvaded). To account for any possible bias in the abundance data, the occupancies (presence or absence) of each native ant species and that of the Argentine ant were also compared between invaded and uninvaded bait stations. All GLZ analyses were performed in STATISTICA for windows, version 7.

Species composition and assemblage structures

Multivariate analyses were performed on both the occupancy and abundance data to compare ant species composition between invaded or uninvaded bait stations in each protected area (using CANOCO version 4.5, Lepš & Šmilauer 2003). Bray-Curtis similarity index (PRIMER version 5, Clarke & Gorley 2001) was used to assess the similarity between bait stations. The Argentine ant was included in the PRIMER analysis. The abundance data were fourth-root transformed before analysis to balance the weight of the contribution by common and rare species (Clarke & Gorley 2001). Thereafter, Analysis of Similarity (ANOSIM, Clarke & Gorley 2001), with status (presence or absence of the Argentine ant) as the main factor was used to determine whether ant assemblage structures differed significantly between invaded and uninvaded bait stations at each nature reserve.

Functional groups

Species were also examined in terms of their functional groups after Andersen (1997a) to determine if the functional group structure differed between invaded and uninvaded bait stations. All the species in the same functional group were grouped together and the proportions of each functional group were compared between invaded and uninvaded bait stations.

Although the functional group approach to classifying ants has only been applied largely in Australia (Andersen 1997a; Majer *et al*. 2004; Hoffman & Andersen 2003), it may also be useful in other parts of the world, particularly as most Australian ant genera are common to Southern Africa (Andersen & Majer 2004).

Multispecies associations and abundance covariation

The association (multispecies presences and absences) between species, and the covariation in species abundances were compared between invaded and uninvaded bait stations using Schluter's (1984) Variance Ratio (VR) tests. Schluter's Variance Ratio test "compares the observed variance in the total number of species or individuals in samples, with the variance expected under the null hypothesis that density or occurrence of each species is independent of the others" (Schluter 1984; Gotelli 2000). To determine whether the presence of the Argentine ant has an effect on species associations and abundance covariations, analyses were done with and without the inclusion of this species in the raw data, and were performed both manually and using Ecosim version 7 (Gotelli & Entsminger 2001). Ecosim was only used to determine species associations, whereas abundance covariation was calculated manually using the formula below (after Schluter (1984)). The obtained VR is then multiplied by N (number of samples) to obtain the test statistic (W) with a chi-square distribution (Schluter 1984; McGeoch & Chown 1997; Gabriel *et al*. 2001). Thus,

$$\sigma_i^2 = p_i(1 - p_i) \qquad \text{… Equation 1}$$

Where $p\text{i} = ni/\text{N}$

$$S_T^2 = (1/N)\sum_j^N (T_j - t)^2 \qquad \text{…Equation 2}$$

where t is the mean number of species per sample.

Therefore, the Variance Ratio,

$$VR = S_T^2 / \sum \sigma_i^2 \qquad \text{…Equation 3}$$

And W is

$W = VR \times N$, with N degrees of freedom …Equation 4

In determining species associations, a positive (> 1) variance ratio (VR) shows that the species in a sample are positively associated, whereas a negative (< 1) variance ratio indicates negative association. If the VR = 1, then there is no association or abundance covariation between species. Similarly, for abundance covariation, a positive variance ratio indicates positive covariation between species, while negative variance ratio indicates negative covariation (Schluter 1984). In a competitively structured community, the observed variance ratio should be significantly smaller than expected by chance for both species associations and abundance covariation (usually less than 1) because of interspecific competition among species (Gotelli & Entsminger 2001). The presence of the Argentine ant inside protected areas could result in the loss of interspecific competition within the native ant community as a result of the biotic homogenization caused by this invasion (Holway & Suarez 2006).

The C-score of Stone and Roberts (1990) was used to determine species co-occurrences at invaded and uninvaded bait stations. Species co-occurrences can be used to determine how ant assemblages are structured at sites invaded and uninvaded by the Argentine ant. The C-score index measures the average number of "checkerboard units" between all possible pairs of species, and is calculated for species that occur at least once in the data matrix (Gotelli & Entsminger 2001; Sanders *et al*. 2003). A checkerboard unit is any submatrix of the form 1 0, 0 1 or 0 1, 1 0 (Gotelli & Entsminger 2001). The analyses were performed in Ecosim version 7, with the Argentine ant included in the raw data. The null model analysis used included fixed rows and equiprobable columns, with 5000 iterations (*sensu* Sanders *et al*. 2003). Thus, the number of checkerboard units (CU) for each species pair is calculated as:

$$CU = (r_i - S)(r_j - S) \quad \text{...Equation 5}$$

Where S is the number of shared sites (sites containing both species) and r_i and r_j are the row totals for species i and j.

Pairwise species correlations

Because the abundance data in this study was not normally distributed, a nonparametric measure of covariation was required for this analysis. I therefore used Spearman's Rank Correlation Coefficient (r_s), widely used in this context (Ludwig & Reynolds 1988), to identify the sign (positive or negative) and test the significance of relationships between Argentine ant abundance and the native ant species abundance occurring across individual bait stations. The correlation coefficient was calculated only for species with a minimum occupancy of 10. Therefore,

$$r_s(i,k) = \frac{\sum y_i(ranked) y_k(ranked)}{\sqrt{\sum y_i^{\,2}(ranked) \sum y_k^{\,2}(ranked)}} \qquad \text{…Equation 6}$$

Beta diversity

Beta diversity was calculated for each protected area to examine the effect of the Argentine ant on native ant community, i.e. the extent of biotic homogenization caused by the Argentine ant. The β_{sim} measure (Lennon *et al*. 2001) was used because it has been shown to be the best method for calculating beta diversity (Koleff *et al*. 2003). Thus,

$$\beta_{sim} = \frac{1}{n}\sum_{i=1}^{n} 1 - S_i ; S_i = \frac{a_i}{a_i + \min(b_i, c_i)} \qquad \text{…Equation 7}$$

where n is the number of pairwise comparisons.

For each pairwise comparison, a is the total number of ant species found at both tetrads, b is the number of species found only in the neighbouring tetrad, while c represents the total number of species found in the focal tetrad and not in its neighbour. β_{sim} indicates

only the difference in species composition and not differences in species richness between the two units being compared (Lennon *et al*. 2001). β_{sim} was calculated for invaded and uninvaded bait stations at each protected area, and also for the protected area as a whole (combining invaded and uninvaded bait stations). General linear models were used to determine whether there were significant differences between invaded and uninvaded bait stations within a protected area, using the variables (1) β_{sim} and (2) the Argentine ant status (invaded or uninvaded), and between protected areas, using the variables (1) β_{sim} and (2) reserve (HNR, JNR, and KBR). Bait stations that were not occupied by any ant species (both native or the Argentine ant) were excluded from the analysis.

RESULTS

Ant species richness and abundances

The ant species collected from all protected areas were a representative sample of the native ant fauna in these areas, as shown by the rarefaction curves approaching an asymptote in all three protected areas (Fig. 1). In total 29 species were collected at bait stations from all three protected areas, with 12 species collected from Helderberg Nature Reserve (HNR), 23 species from Jonkershoek Nature Reserve (JNR) and 14 from Kogelberg Biosphere Reserve (KBR) (Table 2). Seven species, including the Argentine ant, were present at all three reserves, whereas 1, 10, and 4 species were unique to HNR, JNR and KBR respectively (Table 2). There were also significant differences in mean ant species richness for both reserve and status (invaded and uninvaded) (d.f. = 848, deviance = 729.4, scaled deviance/d.f. = 0.86; d.f. (reserve) = 2, X^2 (reserve) = 17.32, d.f. (status) = 1, X^2 (status) = 74.22, $p < 0.001$), based on GLZ analysis with status and reserve as factors. HNR had the lowest mean number of ant species per bait station, whereas KBR had the highest (Fig. 2). There were significantly more species collected at uninvaded versus invaded bait stations across all three protected areas (Fig. 2), and within each protected area (Fig. 3).

There were also significant differences in ant species richness between microhabitats at JNR (d.f. = 420, deviance = 355.85, scaled deviance/d.f. = 0.84; d.f. = 2, X^2 = 39.15, p < 0.001) and KBR (d.f. = 263, deviance = 191.81, scaled deviance/d.f. = 0.72; d.f. = 4, X^2 = 89.58, p < 0.001), but not at HNR (d.f. = 2, X^2 = 2.13, p = 0.34) (Fig. 4). The lowest abundance of native ant species occurred in areas around buildings, with the Argentine ant being the only species collected at this microhabitat at HNR and JNR (however there were very few bait stations placed at this microhabitat at JNR, see Table 1) (Fig. 4). Although some native ant species were collected from around buildings at KBR, ant species richness was very low at this microhabitat compared with other microhabitats (Fig. 4). Lawn was the second most impacted microhabitat, with all bait stations occupied only by the Argentine ant at HNR. On average, HNR had the lowest mean number of ant species in all microhabitats, whereas KBR had the highest mean species richness, with all five microhabitats occupied by native ant species (Fig. 4). Microhabitats with high Argentine ant abundance had low ant species richness, while microhabitats with low Argentine ant abundance had high species richness (Fig. 4).

The Argentine ant was the most abundant species at invaded bait stations at all three protected areas (Fig. 5). *Pheidole capensis* dominated uninvaded bait stations at JNR and KBR (Fig. 5), whereas *Anoplolepis custodiens*, followed by *A. steingroeveri* were the two most abundant ant species at the uninvaded bait stations at HNR (Fig. 5). Although *Pheidole capensis* and *Pheidole* sp. 5 occurred at invaded bait stations together with the Argentine ant, the abundance of the Argentine ant was significantly higher than the abundances of *P. capensis* (d.f. = 691, deviance = 21119.50, scaled deviance/d.f. = 30.56; d.f. = 1, X^2 = 121.61, p < 0.001) and *Pheidole* sp. 5 (d.f. = 424, deviance = 2112.53, scaled deviance/d.f. = 4.98; d.f. = 1, X^2 = 41.86, p < 0.001) (Table 3). The abundances of most native ant species were higher at uninvaded than invaded bait stations, however, abundances of *M. peringueyi*, *T. quadrispinosum* and *Monomorium* sp. 8 were not significantly different between invaded and uninvaded bait stations (Table 4). The overall mean ant abundances (both native ants and the Argentine ant) were much higher in the presence of the Argentine ant (Table 4). No native ant species were significantly more abundant at invaded compared with uninvaded bait stations (Table 4). Relative ant

species occupancies (presence or absence) at invaded and uninvaded bait stations showed a similar pattern to the relative abundances at all three protected areas (Fig. 6).

Species composition and assemblage structures

The percentage variance in ant assemblage structure explained by both axes for the combined data of all three protected areas was low (4.5 %), although both canonical axes explained a significant amount of variation in the ant assemblage structure (F-ratio = 7.699, $p < 0.001$) (Fig. 7A). Ant assemblage structures were also significantly different between invaded and uninvaded bait stations at all three protected areas ($p < 0.001$), with Global R values of 0.993, 0.616 and 0.548 for HNR, JNR and KBR respectively. At HNR, canonical axes did not explain a significant amount of variation in the assemblage structure ($F = 1.488$, $p = 0.147$), and the percentage variance explained by both axes was 17.2 % (Fig. 7B). At JNR, the amount of variation explained by both canonical axes was significant ($F = 7.864$, $p < 0.001$) with the total variability in the data explained by 10.3 % (Fig. 7C), and at KBR ($F = 5.171$, $p < 0.001$), with both axes explaining 14.4 % of the variability in the data (Fig. 7D). Of the 29 species collected, three species (*Meranoplus peringueyi*, *Tetramorium quadrispinosum* and *Monomorium* sp. 8), were positively associated with the presence (at invaded bait stations) of the Argentine ant at all three protected areas (Fig. 7). Overall, there was a significant difference in species composition and assemblage structures between invaded and uninvaded bait stations at all three protected areas.

Functional groups

The 29 species collected in this study belonged to nine different functional groups (Table 2; Fig. 8). The Argentine ant was the only species collected in this study belonging to the Dominant Dolichoderine functional group (this functional group is not part of the native South African ant fauna (Majer *et al*. 2004)). Generalized Myrmicinae was the most common functional group with 10 (34.5 %) of the 29 species collected belonging to this group. This functional group was well represented at both invaded and uninvaded bait

stations at all three protected areas (Fig. 8). The second richest function group, with 20.7 % of the species collected belonging to it, was the Opportunists (Fig. 8). Only one species in the functional group Cold Climate Specialists (*Leptothorax* sp. 1) was collected at the uninvaded bait stations from JNR. *Pachycondyla pumicosa* was the only species collected in the functional group Specialized Predator and was also collected at uninvaded bait stations (Fig. 8).

Multispecies association, abundance covariation and pairwise species correlations

At the uninvaded bait stations, ant species were negatively associated with each other (VR < 1.0; C-score: observed value > expected value) at all three protected areas; however, the association was only significant at JNR (Table 5). At invaded bait stations species were significantly positively associated at all three reserves (Table 5). On the other hand, at JNR, the abundance of species covaried positively at both invaded and uninvaded bait stations, but the covariation was only significant at the uninvaded bait stations (Table 5). Helderberg Nature Reserve had negative, but non-significant, abundance covariation for both invaded and uninvaded bait stations, whereas KBR had positive, and significant, abundance covariation for both invaded and uninvaded bait stations (Table 5). There was no relationship between Variance Ratio and ant abundance when the Argentine ant was included in the total ant abundance (Fig. 9A). There was a very slight tendency for high Variance Ratios in native ant communities at uninvaded bait stations (Fig. 9B). The variance ratio may be sensitive to ant abundances to some extent. The abundances of three species: *Crematogaster* sp. 3 (at JNR), *Camponotus* sp. 1 and *Tetramorium quadrispinosum* (at KBR), were positively correlated with the Argentine ant (Table 6), but *Crematogaster* sp. 3 was the only species that was significantly positively correlated with the Argentine ant (Table 6). On the other hand, the abundances of several species, *Ocymyrmex barbiger* (at HNR), *Anoplolepis custodiens*, *A. steingroeveri*, *Pheidole capensis*, *Pheidole* sp. 5, *T. quadrispinosum* (at JNR), *Lepisiota* sp. 1, and *P. capensis* (at KBR) were significantly negatively correlated with the abundance of the Argentine ant (Table 6).

Beta diversity

There were significant differences in ant species compositional turnover between reserves (d.f. = 2, 42206; F = 1471.35; $p < 0.001$). Overall, HNR had the lowest β_{sim} value for the entire reserve, while β_{sim} was similar for JNR and KBR (Table 7). There were also significant differences in species turnover between invaded and uninvaded bait stations at HNR (d.f. = 1, 7034; F = 26916.32; $p < 0.001$), at JNR (d.f. = 1, 24202; F = 56831.54; $p < 0.001$) and at KBR (d.f. = 1, 10967; F = 8976.3; $p < 0.001$). Mean beta diversity (β_{sim}) was higher at uninvaded bait stations at all three protected areas (Table 7).

DISCUSION

Ant species richness and abundances

Several native ant species are displaced by the Argentine ant in several parts of the world (Erickson 1971; Ward 1987; Reimer 1994; Human & Gordon 1996; Holway 1999). Here, I identified a number of species that are displaced by the Argentine ant in all three protected areas. Two species in particular (*Anoplolepis* sp. 3 and *A. steingroeveri*) were severely negatively affected by the presence of the Argentine ant at JNR and HNR, and were only present and abundant at uninvaded bait stations. The species richness at individual bait stations was also very low (*ca*. 60 % lower) in the presence of the Argentine ant. Jonkershoek Nature Reserve had higher species richness than KBR (23 versus 14 species), despite that KBR is a much larger reserve in size than JNR. Helderberg Nature Reserve, the smallest of the three reserves, had similar species richness (12 species) to KBR. This is probably the result of the dominance by one native ant species, *Pheidole capensis*, throughout most of KBR. Bond and Slingsby (1984) found that *P. capensis* was completely displaced from areas invaded by the Argentine ant at KBR. Similarly, other studies also found that *P. capensis* was displaced from invaded sites at JNR (De Kock 1990; Witt & Giliomee 1999). In this study, *P. capensis* was only found at bait stations unoccupied by the Argentine ant at all three protected areas, thus these results were consistent with previous studies.

The variance in species richness amongst uninvaded bait stations was lower than expected from the null model, resulting in negative species associations. Therefore, this was evidence that the native ant assemblage at baits at all three nature reserves was competitively structured. Conversely, variance in species richness amongst invaded bait stations was higher than expected, resulting in positive species associations and the loss of competition within the ant assemblage. Similarly, Sanders *et al*. (2003) found that the presence of the Argentine ant resulted in the loss of competition within invaded communities. Negative association often occurs as a result of interference competition when resources such as food are limited, with species occasionally excluding each other and resulting in negatively covarying population sizes (Schluter 1984). This type of association (negative) can be expected, particularly in competitively structured communities (Gotelli & Entsminger 2001). Interference competition is common in ant communities (Hölldobler & Wilson 1990), and plays a major role in structuring ant communities (Lach 2005; Sarty *et al*. 2006). Interference competition is also likely to be more evident when using bait traps rather than pitfall traps, because ant species with the same resources compete directly for the available food over a short period.

Despite the displacement by the Argentine ant, a few native ant species, e.g. *M. peringueyi*, *T. quadrispinosum* and *Monomorium* sp. 8 were found co-occurring with this species at all three protected areas. For some ant species, this pattern could suggest that they are only temporarily co-occurring with the Argentine ant in recently invaded areas, and will eventually be eliminated from these areas (Holway 1999; Wetter *et al*. 2001). For example, *Anoplolepis custodiens* was found at both invaded and uninvaded bait stations at HNR, whereas this species was only found at uninvaded bait stations at the other two protected areas. This species was found at the edge between the invaded and uninvaded zone at HNR and may also eventually disappear from invaded sites. Biotic resistance, as well as other physical factors such as soil type, could play a role in limiting the spread of the Argentine ant into areas dominated by *A. custodiens* (Way 1987; Way *et. al*. 1997). This demonstrates spatial and possibly also temporal variability in the impact of the Argentine ant. Previous studies have shown that *A. custodiens* has been completely displaced from invaded sites by the Argentine ant at JNR (De Kock 1990; Witt & Giliomee 1999) and at KBR (Bond & Slingsby 1984; Christian 2001).

While most native ant species at all three protected areas were negatively correlated with the presence of the Argentine ant, some were positively correlated with its presence. These positively correlated species have different phenologies to that of the Argentine ant and do not particularly interact directly with it. For example, *Crematogaster* species are arboreal (they forage on tree trunks) while Argentine ants are generally epigaeic (they forage above ground, although they have been found foraging on vineyards and Protea plants (Addison & Samways 2000; N.M. Luruli, personal observation)), and therefore these species can occur within the same area due to their different foraging habits and nesting preferences. Other species that were positively correlated with the Argentine ant are the *Camponotus* species. Species belonging to this genus have large body sizes and they are often behaviourally submissive to Argentine ants (Andersen 1997a). A positive correlation between the Argentine ant and other native ant species implies that when the abundance of the Argentine ant increases at a bait station, there is a corresponding increase in the abundance of the native ant with which it coexists (Ludwig & Reynolds 1988). Similarly, a negative correlation implies that for an increase in the abundance of the Argentine ant, there is a decrease in the abundance of the coexisting native ant (Ludwig & Reynolds 1988). Thus, in this study, the abundances of most native ant species were severely reduced when abundances of the Argentine ant are high.

In this study, the Argentine ant dominated the invaded tuna baits in most cases, and often recruited to the bait more quickly than any other native ant species (N.M. Luruli, personal observation). The large abundances of the Argentine ant at bait stations resulted in the decrease in the abundances of native ants occurring with it, however, some species were more affected than others. This trend has also been shown by some previous work (Human & Gordon 1996). Changes in resource availability may result in positive abundance covariation between species competing for identical, limited resources (McGeoch & Chown 1997). The level of abundance covariation was higher at uninvaded than invaded bait stations at all three protected areas, and was significant at JNR and KBR. By contrast, species abundances covaried significantly (and positively) only at KBR. This corresponds to the degree of impact of the Argentine ant on native ant community at the three protected areas (greatest at HNR and smallest at KBR). In other words, where native communities remain comparatively intact, species abundances tend

to covary positively, whereas the greater the extent of invasion by the Argentine ant, the less likely that species abundances will covary, as a consequence of the generally low abundance of native species. Thus, results of this study suggest that the native ant community at all three protected areas is competitively structured, and the presence of the Argentine ant results in the loss of these competitive interactions by swamping of native communities and local extinction of native species caused by the Argentine ant.

In California, water availability and human activities have been shown to influence the distribution and spread of Argentine ants within an area (Suarez *et al*. 1998; Holway 1998a; Holway *et al*. 2002). This suggests that any ant species occurring at areas around water sources and buildings are particularly vulnerable to displacement by the Argentine ant. In a study conducted in Spain, Carpintero *et al*. (2003) found the Argentine ant in close perimeters to occupied houses, and these houses were situated in various habitat types. In this study, areas around buildings and lawn were the most impacted by the presence of the Argentine ant, and these microhabitats had very low native ant species richness.

Species composition and assemblage structure

While most native ant species in this study were displaced by the Argentine ant, some species, particularly *Meranoplus peringueyi*, *Tetramorium quadrispinosum* and *Monomorium* sp. 8, were found co-occurring with it. However, all these ant species were less abundant than the Argentine ant at invaded bait stations at HNR and JNR, and more abundant than the Argentine ant at invaded bait stations at KBR. On average, the abundances of *M. peringueyi*, *T. quadrispinosum* and *Monomorium* sp. 8 were higher at uninvaded than invaded bait stations. Therefore, this study suggests that although these three species are able to survive in the presence of the Argentine ant, their abundances are negatively affected. This finding is consistent with previous research conducted by Christian (2001) at KBR, where she found *T. quadrispinosum* and *M. peringueyi* in the same pitfall traps with the Argentine ant. Similarly, Addison and Samways (2000) found *T. quadrispinosum* wherever the Argentine ant occurred in vineyards in the Western Cape Province.

The ability of native ant species to coexist with the Argentine ant can be attributed to several factors, including habitat selection, resource utilization and the ability of a species to defend itself from predators (Andersen *et al*. 1991; Human & Gordon 1996; Holway 1999). Species in the genera *Tetramorium* are opportunist, which are generally found in areas with low ant diversity, and have the ability to coexist with the Argentine ant (Hoffmann & Andersen 2003). *Tetramorium quadrispinosum* in particular has a habit of closing its nest entrance to protect itself from invasion (Witt & Giliomee 1999). *Monomorium* sp. 8 is in the functional group Generalized Myrmicinae, and species in this functional group are often able to find and successfully defend food resources (Hoffman & Andersen 2003). Many *Monomorium* species are also able to repel attacks from Argentine ants by spraying it with their defensive, chemical secretions (Andersen *et al*. 1991). For example, an experiment conducted by Holway (1999) in northern California showed that *Monomorium ergatogyna* was successful in overcoming attacks by the Argentine ant through spraying their highly repellent chemical compounds on the Argentine ant workers. From most parts of the globe, the genera *Meranoplus* is known to occur in areas where dominant Dolichoderines (like the Argentine ant) are not abundant (Andersen 2000), but in this study *Meranoplus peringueyi* was found co-occuring with the Argentine ant. As shown elsewhere in the world (Erickson 1971; Ward 1987; Holway 1999; DiGirolamo & Fox 2006), this study confirms that the Argentine ant has serious negative consequences not only for the presence, but also the abundances of the native ant community of invaded areas.

Most functional groups in this study were present at both invaded and uninvaded bait stations, and thus the presence of the Argentine ant in the protected areas in this study did not have a large impact on the functional group composition visiting bait stations. Generalized myrmicines were present at both invaded and uninvaded bait stations, with four species found at both invaded and uninvaded bait stations. Species belonging to this functional group have generalist nesting sites and resource requirements (Andersen 1997a), which enable them to obtain enough resources in the presence of the Argentine ant and are therefore able to coexist with it (Walters 2006). Opportunists were also well represented at both invaded and uninvaded bait stations, with three species occurring at both invaded and uninvaded bait stations. The Cold Climate Specialists were represented

by only one species (*Leptothorax* sp. 1), and was collected in the absence of the Argentine ant. Species in this functional group forage in cooler environments where the activity of the Argentine ant is lower, and they are generally considered to avoid direct interaction with the Argentine ant (Andersen 1997a). In a previous study conducted in Adelaide, South Australia, Walters (2006) collected the Cold Climate Specialists species during the cooler months (May and September), and this group was not collected during the summer and autumn periods (using pitfall traps). Specialized Predators have specialized diets, they have large body sizes and often occur in low population sizes (Andersen 1997a). Functional groups have been largely applied in Australia to determine the response of ant communities to disturbance (Andersen 1997b; Hausner *et al*. 2003). However, it is important to note that the functional group scheme was designed for the analyses of ant communities across biogeographical scales, rather than for detailed studies of local ant community dynamics (Andersen 1997b; Hoffmann & Andersen 2003). Therefore, the use of functional groups at a local scale may not produce reliable information about changes in the ant community. Also, the functional group system uses the ant generic level and not the species level, and therefore any impacts on individual ant species will be missed.

The ant assemblage structure of invaded ant communities was significantly different to that of uninvaded communities, and HNR and JNR had more similar ant species composition to each other than with KBR. The fact that these two protected areas are geographically closer to each other (ca. 15 km apart) than they are to KBR (ca. 50 km away) may result in ant communities being shared between the two reserves. At HNR, the structure of the ant community was strongly related to the presence or absence of the Argentine ant, and most native ant species were found in the absence of the Argentine ant. Native ant species that were found at invaded bait stations (co-occuring with the Argentine ant) were common at all three protected areas, i.e. *M. peringueyi*, *T. quadrispinosum* and *Monomorium* sp. 8. Ant species compositional turnover between individual bait stations was very low at invaded bait stations at all protected areas. Uninvaded bait stations contained eight times more native ant species than invaded bait stations. This was a result of the dominance of bait stations by the Argentine ant, while uninvaded bait stations contained, on average, more than one ant species. The mean beta

diversity (β_{sim}) obtained at all three protected areas in this study, particularly at uninvaded bait stations, was generally high compared with the mean β_{sim} obtained from previous studies (Lennon *et al*. 2001; Koleff & Gaston 2002; Boonzaaier 2006). This means that in this study there was a high species turnover between bait stations at uninvaded sites, while species turnover between bait stations at invaded sites was, on average, zero. Thus, beta diversity was reduced by almost 100 % at invaded sites at all three protected areas, resulting in the biotic homogenization of the local ant community. In California, Holway and Suarez (2006) also found evidence of biotic homogenization in sites invaded by the Argentine ant, with most epigaeic ant species displaced by the Argentine ant.

A study conducted by Boonzaaier (2006) at HNR and JNR using pitfall traps found higher species richness at both protected areas than the current study (one and half times and almost twice as many ant species at HNR and JNR respectively). The pitfall traps were left open for five consecutive days, while bait stations in this study were open only for one hour during the day. Therefore ant species with different foraging times, i.e. diurnal and nocturnal foragers, will be collected in the same pitfall traps although they do not necessarily co-exist with each other and may portray temporal niche separation. Although baits were used to sample ants in this study, the ant species collected are a large proportion of the species in these protected areas. For example, 23 species were collected from JNR in this study, while 34 species were collected by Boonzaaier (2006), 33 and 31 collected by De Kock (1990) and Schlettwien & Giliomee (1987) respectively from the same nature reserve. Ants were sampled using pitfall traps in all the above studies. Unfortunately, no ant species lists were available from HNR and KBR for comparison. Also, some species collected in this study were not collected in any of the previous studies. For example, Boonzaaier (2006) collected two *Pheidole* species, whereas five *Pheidole* species were collected in this study. *Anoplolepis* sp. 3, which was collected at both HNR and JNR in this study, has also not been recorded from these areas before the current study.

The findings of this study were consistent with those of studies conducted elsewhere in the world (Erickson 1971; Ward 1987; Human & Gordon 1996). Native ant species diversity and composition was severely reduced at all three protected areas due to the

Argentine ant invasion, resulting in significant biotic homogenization of native ant communities by the Argentine ant. Thus, species turnover between bait stations at invaded sites was reduced to almost zero at all three protected areas. Although many native ant species were displaced by the Argentine ant, few species were able to coexist with it, but their abundances were reduced at invaded bait stations. The impact of the Argentine ant on native ant communities was evident across all three protected areas, however, HNR was the most impacted (with the lowest species richness and species turnover), followed by JNR and then KBR. Areas characterized by high human activities, i.e. buildings and lawn areas, were the most severely affected habitat types, with the least number of native ant species. In conclusion, the Argentine ant has a significant negative impact on the species richness, species turnover and assemblage structure of the local native ant communities of the three protected areas.

REFERENCES

ADDISON, P. & SAMWAYS, M.J. 2000. A survey of ants (Hymenoptera: Formicidae) that forage in vineyards in the Western Cape Province, South Africa. *African Entomology* **8**: 251-260.

ANDERSEN, A.N., BLUM, M.S. & JONES, T.H. 1991. Venon alkaloids in *Monomorium* "*rothsteini*" Forel repel other ants: is this the secret to success of *Monomorium* in Australian ant communities? *Oecologia* **88**: 157-160.

ANDERSEN, A.N. 1997a. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. *Journal of Biogeography* **24**: 433-460.

ANDERSEN, A.N. 1997b. Using ants as bioindicators: multi-scale issues in ant community ecology. Conservation Ecology 1(8) (online). Available from http//www. Consecol.org/vol1/iss1/art8.

ANDERSEN, A.N. 2000. Global ecology of rainforest ants: functional groups in relation to environmental stress and disturbance. In: Agosti, D., Majer, J.D., Alonso, L.E. & Schultz, T.R. (Eds). *Ants*: *standard methods for measuring and monitoring biodiversity*. 25-34. Smithsonian Institution Press, Washington, London.

ANDERSEN, A.N., HOFFMANN, B.D., MÜLLER, W.J. & GRIFFITHS, A.D. 2002. Using ants as bioindicators in land management: simplifying assessment of ant community responses. *Journal of Applied Ecology* **39**: 8-17.

ANDERSEN, A.N. & MAJER, J.D. 2004. Ants show the way down under: invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* **2**: 291-298.

BESTELMEYER, B.T. 1997. Stress tolerance in some Chacoan dolichoderine ants: implications for community organization and distribution. *Journal of Arid Environments* **35**: 297-310.

BESTELMEYER, B.T., AGOSTI, D., ALONSO, L.E., ROBERTO, C., BRANDAO, F., BROWN, W.L. (Jr)., DELABIE, J.H.C., & SILVESTRE, R. 2000. Field techniques for the study of ground-dwelling ants. In: Agosti, D., Majer, J.D., Alonso, L.E. & Schultz, T.R. (Eds). *Ants*: *standard methods for measuring and*

monitoring biodiversity. 122-144. Smithsonian Institution Press, Washington, London.

BLANCAFORT, X. & GÓMEZ, C. 2005. Consequences of the Argentine ant, *Linepithema humile* (Mayr), invasion on pollination of *Euphorbia characias* (L.) (Euphorbiaceae). *Acta Oecologica* **28**: 49-55.

BOND, W.J. & SLINGSBY, P. 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *South African Journal of Science* **79**: 231-223.

BOND, W.J. & SLINGSBY, P. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorus Proteaceae. *Ecology* **65**: 1031-1037.

BOND, W.J. & BREYTENNACH, G.J. 1985. Ants, rodents and seed predation in Proteaceae. *South African Journal of Zoology* **20**:150-154.

BOND, W.J. & STOCK, W.D. 1989. The costs of leaving home: ants disperse myrmecochorus seeds to low nutrient sites. *Oecologia* **81**: 412-417.

BOONZAAIER, C. 2006. *Conservation in human-influenced areas*: *epigaeic arthropods in the Cape Floristic Region lowlands*. MSc Thesis, University of Stellenboch, Stellenbosch.

BOTES, A., MCGEOCH, M.A., ROBERTSON, H.G., VAN NIEKERK, A., DAVIDS, H.P. & CHOWN, S.L. 2006. Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* **33**: 71-90.

BOUCHER, C. 1978. Cape Hangklip area. II. The vegetation. *Bothalia* **12**: 455-497.

BROWN, W.L. (Jr). 2000. Diversity of ants. In: Agosti, D., Majer, J.D., Alonso, L.E. & Schultz, T.R. (Eds). *Ants*: *standard methods for measuring and monitoring biodiversity*. 45-79. Smithsonian Institution Press, Washington, London.

CARNEY, S.E., BYERLEY, M.B. & HOLWAY, D.A. 2003. Invasive Argentine ants (*Linepithema humile*) do not replace native ants as seed dispersers of *Dendromecon rigida* (Papaveraceae) in California, USA. *Oecologia* **135**: 576-582.

CARPINTERO, S., REYES-LÓPEZ, J. & ARIAS DE REYNA, L. 2003. Impact of human dwellings on the distribution of the exotic Argentine ant: a case study in the Doñana National Park, Spain. *Biological Conservation* **115**: 279-289.

CERDA, X., RETANA, J. & MANZANEDA, A. 1998. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. *Oecologia* **117**: 404-412.

CHRISTIAN, C.E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* **413**: 635-639.

CLARKE, K.R. & GORLEY, R.N. 2001. PRIMER v5: user manual/tutorial. PRIMER-E Ltd.

COLE, F.R., MEDEIROS, A.C., LOOPE, L.L., & ZUEHLKE, W.W. 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology* **73**: 1313-1322.

COWLING, R.M. & HOLMES, P.M. 1992. Plant diversity and endemism. In: Cowling, R.M. (Ed). *The ecology of Fynbos: nutrients, fire and diversity*. 62-112. Oxford University Press, Cape Town.

CROWELL, K.L. 1968. Rates of competitive exclusion by the Argentine ant in Bermuda. *Ecology* **49**: 551-555.

DE KOCK, A.E. 1990. *The Argentine ant,* Iridomyrmex humilis *Mayr, indigenous ants and other epigaeic invertebrates of the Fynbos in relation to fire and vegetation age*. MSc Thesis, University of Stellenboch, Stellenbosch.

DIGIROLAMO, L.A. & FOX, L.R. 2006. The influence of abiotic factors and temporal variation on local invasion patterns of the Argentine ant (*Linepithema humile*). *Biological Invasions* **8**: 125-135.

DOBSON, A.J. 2002. An introduction to generalized linear models. Chapman and Hall.

ELTON, C.S. 1958. *The ecology of invasions by animals and plants*. Methuen, London.

ERICKSON, J.M. 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. *Psyche* **78**: 257-266.

FISHER, R.N., SUAREZ, A.V. & CASE, T.J. 2002. Spatial patterns in the abundance of the coastal horned lizard. *Conservation Biology* **16**: 205-215.

FLUKER, S.S. & BEARDSLEY, J.W. 1970. Sympatric associations of three ants: *Iridomyrmex humilis*, *Pheidole megacephala*, and *Anoplolepis longipes* in Hawaii. *Annals of the Entomological Society of America* **63**: 1290-1296

GABRIEL, A.G.A., CHOWN, S.L., BARENDSE, J., MARSHALL, D.J., MERCER, R.D., PUGH, P.J.A. & SMITH, V.R. 2001. Biological invasions of Southern Ocean Islands: the collembola of Marion Island as a test of generalites. *Ecography* **24**: 421-430.

GOTELLI, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**: 2606-2621.

GOTELLI, N.J. & ENTSMINGER, G.L. 2001. Ecosim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/Ecosim.htm.

GOTELLI, N.J. & COLWELL, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**: 379-391.

HASKINS, C.P. & HASKINS, E.F. 1965. *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda – equilibrium or slow replacement? *Ecology* **46**: 736-740.

HASKINS, C.P. & HASKINS, E.F. 1988. Final observasions on *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda. *Psyche* **95**: 177-184.

HAUSNER, V.H., YOCCOZ, N.G. & IMS, R.A. 2003. Selecting indicator traits for monitoring land use impacts: birds in northern coastal birch forests. *Ecological Applications* **13**: 999-1012.

HOFFMANN, B.D. & ANDERSEN, A.N. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* **28**: 444-464.

HÖLLDOBLER, B. & WILSON, E.O. 1990. *The ants*. Harvard University Press, Cambridge, Massachusetts.

HOLWAY, D.A. 1995. Distribution of the Argentine ant (*Linepithema humile*) in Northern California. *Conservation Biology* **9**: 1634-1637.

HOLWAY, D.A. 1998a. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia* **116**: 252-258.

HOLWAY, D.A. 1998b. Factors governing rate of invasion: a natural experiment using Argentine ants. *Oecologia* **115**: 206-212.

HOLWAY, D.A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* **80**: 238-251.

HOLWAY, D.A., LACH, L., SUAREZ, A.V., TSUTSUI, N.D. & CASE, T.J. 2002. The causes and consequences of ant invasions. *Annual Review of Ecological Systematics* **33**: 181-233.

HOLWAY, D.A. & SUAREZ, A.V. 2004. Colony-structure variation and interspecific competitive ability in the invasive Argentine ant. *Oecologia* **138**: 216-222.

HOLWAY, D.A. & SUAREZ, A.V. 2006. Homogenization of ant communities in Mediterranean California: the effects of urbanization and invasion. *Biological Conservation* **127**: 319-326.

HUMAN, K.G. & GORDON, D.M. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* **105**: 405-412.

HUMAN, K.G. & GORDON, D.M. 1999. Behavioral interactions of the invasive Argentine ant with native ant species. *Insectes Sociaux* **46**: 159-163.

JOHNS, A. & JOHNS, M. 2001. *Kogelberg Biosphere Reserve*: heart of the Cape flora. Struik Publishers.

JOHNSON, S.D. 1992. Plant-animal relationships. In: Cowling, R.M. (Ed). *The ecology of Fynbos*: *Nutrients, fire and diversity*. 175-205. Oxford University Press, Cape Town.

KOLEFF, P. & GASTON, K.J. 2002. The relationship between local and regional species richness and spatial turnover. *Global Ecology and Biogeography* **11**: 363-375.

KOLEFF, P., GASTON, K.J. & LENNON, J.J. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* **72**: 367-382.

LACH, L. 2005. Interference and exploitation competition of three nectar-thieving invasive ant species. *Insectes Sociaux* **52**: 257-262.

LE MAITRE, D.C., VAN WILGEN, B.W., CHAPMAN, R.A. & MCKELLY, D.H. 1996. Invasive plants and water resources in the Western Cape Province, South

Africa: modeling the consequences of a lack of management. *Journal of Applied Ecology* **33**: 161-172.

LENNON, J.J., KOLEFF, P., GREENWOOD, J.J.D. & GASTON, K.J. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* **70**: 966-979.

LEPŠ, J. & ŠMILAUER, P. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge.

LOWE, S., BROWNE, M., BOUDJELAS, S. & DE POORTER, M. 2000. 100 of the world's worst invasive alien: a selection from the Global Invasive Species Database. *The Invasive Species Specialist Group (ISSG), World Conservation Union (IUCN)*.

LUDWIG, J.A. & REYNOLDS, J.F. 1988. Statistical ecology: a primer on methods and computing. Wiley-Interscience Publication.

MAJER, J.D. 1994. Spread of Argentine ants (*Linepithema humile*), with special reference to Western Australia. In: Williams, D.F. (Ed). *Exotic ants*: *biology, impact and control of introduced species*. 121-132. Westview Press, Colorado, USA

MAJER, J.D., SHATTUCK, S.O., ANDERSEN, A.N. & BEATTIE, A.J. 2004. Australian ant research: fabulous fauna, functional groups, pharmaceuticals, and the fatherhood. *Australian Journal of Entomology* **43**: 235-247.

MARKIN, G.P. 1970. The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae), in Southern California. *Annals of the Entomological Society of America* **63**: 1238-1242.

MCGEOCH, M.A. & CHOWN, S.L. 1997. Evidence of competition in a herbivorous, gall-inhabiting moth (Lepidoptera) community. *Oikos* **78**: 107-115.

MOLL, E.J. & JARMAN, M.L. 1984. Clarification of the term Fynbos. *South African Journal of Science* **80**: 351-352.

NETSHILAPHALA, N.M., MILTON, S.J. & ROBERTSON, H.G. 2005. Response of an ant assemblage to mining on the arid Namaqualand coast, South Africa. *African Entomolgogy* **13**: 162-167.

PARR, C.L., ROBERTSON, H.G., BIGGS, H.C. & CHOWN, S.L. 2004. Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology* **41**: 630-642.

PASSERA, L. 1994. Characteristics of tramp species. In: Williams, D.F. (Ed). *Exotic ants*: *biology, impact and control of introduced species*. 23-43. Westview Press, Colorado, USA

PORTER, S.D. & SAVIGNANO, D.A. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* **71**: 2095-2106.

PRINS, A.J., ROBERTSON, H.G. & PRINS, A. 1990. Pest ants in urban and agricultural areas of Southern Africa. In: Vander Meer, R.K., Jaffe, K, & Cedeno, A. (Eds). *Applied myrmecology*: *a world perspective*. 25-33. Westview Press, Colorado, USA.

REIMER, N.J. 1994. Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. In: Williams, D.F. (Ed.). *Exotic ants: Biology, Impact, and control of introduced species*. 11-22. Westview Press, Boulder, Colorado.

SAMWAYS, M.J., NEL, M. & PRINS, A.J. 1982. Ants (Hymenoptera: Formicidae) foraging in the citrus trees and attending honeydew-producing homoptera. *Phytophylaciica* **14**: 155-157.

SANDERS, N.J., GOTELLI, N.J., HELLER, N.E. & GORDON, D.M. 2003. Community disassembly by an invasive species. *Proceedings of the National Academy of Science* **100**: 2474-2477.

SARTY, M., ABBOTT, K.L. & LESTER, P.J. 2006. Habitat complexity facilitates coexistence in a tropical ant community. *Oecologia* **149**: 465-473.

SCHLETTWEIN, C.H.G. & GILLIOMEE, J.H. 1987. Comparison of insect biomass and community structure between Fynbos sites of different ages after fire with particular reference to ants, leafhoppers and grasshoppers. *Annale Universiteit van Stellenbosch* 2 (2), Serie A3 (Landbouwetenskappe).

SCHLUTER, D. 1984. A variance test for detecting species associations, with some example applications. *Ecology* **65**: 998-1005.

SLINGSBY, P. & BOND, W. 1981. Ants – friends of the Fynbos. *Veld and Flora* **67**: 39-45.

STONE, L. & ROBERTS, A. 1990. The checkerboard score and species distributions. *Oecologia* **85**: 74-79.

SUAREZ, A.V., BOLGER, D.T. & CASE, T.J. 1998. Effects of fragmentation and invasion on native ant communities in coastal Southern California. *Ecology* **79**: 2041-2056.

SUAREZ, A.V., HOLWAY, D.A. & CASE, T.J. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proceedings of the National Academy of Science* **98**: 1095-1100.

SUAREZ, A.V. & CASE, T.J. 2002. Bottom-up effects on persistence of a specialist predator: ant invasions and horned lizards. *Ecological Applications* **12**: 291-298.

SUAREZ, A.V., YEH, P. & CASE, T.J. 2005. Impacts of Argentine ants on avian nesting sites. *Insectes Sociaux* **52**: 378-382.

SUTHERLAND, J. 1996. *Ecological census techniques – a handbook*. Cambridge University Press, UK.

TSUTSUI, N.D. & SUAREZ, A.V. 2003. The colony structure and population biology of invasive species. *Conservation Biology* **17**: 48-58.

THOMAS, M.L. & HOLWAY, D.A. 2005. Condition-specific competition between invasive Argentine ants and Australian *Iridomyrmex*. *Journal of Animal Ecology* **74**: 532-542.

VAN WILGEN, B.W. & RICHARDSON, D.M. 1985. The effects of alien shrub invasions on vegetation structure and fire behaviour in South African Fynbos shrublands: a simulation study. *Journal of Applied Ecology* **22**: 955-966.

VAN WYK, A.E. & SMITH, G.F. 2001. *Regions of floristic endemism in Southern Africa*: *a review with emphasis on succulents*. Umdaus Press.

WALTERS, A.C. & MACKAY, D.A. 2005. Importance of large colony size for successful invasion by Argentine ants (Hymenoptera: Formicidae): Evidence for biotic resistance by native ants. *Austral Ecology* **30**: 395-406.

WALTERS, A.C. 2006. Invasion of Argentine ants (Hymenoptera: Formicidae) in South Australia: impacts on community composition and abundance of invertebrates in urban parklands. *Austral Ecology* **31**: 567-576.

WARD, P.S. 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. *Higardia* **55**: 1-16.

WETTERER, J.K., WETTERER, A.L. & HEBARD, E. 2001. Impact of the Argentine ant, *Linepithema humile* on native ants of Santa Cruz Island, California. *Sociobiology* **38**: 709-721.

WHITE, E.M., WILSON, J.C. & CLARKE, A.R. 2006. Biotic indirect effects: a neglected concept in invasion biology. *Diversity and Distributions* **12**: 443-455.

WICHT, C.L., MEYBURGH, J.C. & BOUSTEAD, P.G. 1969. Rainfall at the Jonkershoek Forest Hydrological Research Station. *Annale Universiteit van Stellenbosch* 44, Serie A(1).

WITT, A.B.R. 1993. *Factors affecting myrmecochory in Fynbos*. MSc Thesis, University of Stellenbosch, Stellenbosch.

WITT, A.B.R. & GILIOMEE, J.H. 1999. Soil-surface temperatures at which six species of ants (Hymenoptera: Formicidae) are active. *African Entomology* **7**: 161-164.

WITT, A.B.R., GEERTSEMA, H. & GILIOMEE, J.H. 2004. The impact of an invasive ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), on the dispersal of the elaiosome-bearing seeds of six plant species. *African Entomology* **12**: 223-230.

ZEE, J. & HOLWAY, D. 2006. Nest raiding by the invasive Argentine ant on colonies of the harvester ant, *Pogonomyrmex subnitidus*. *Insectes Sociaux* **53**: 161-167.

Table1. Total number of bait stations placed in each microhabitat at three protected areas (and total bait stations in each reserve). There is no lawn area inside JNR, and thus no samples were collected in this microhabitat type. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve and KBR = Kogelberg Biosphere Reserve.

Microhabitat	HNR	JNR	KBR
Buildings	14	3	38
Lawn	30	-	30
Road	54	202	30
Vegetation	31	166	155
Waterbodies	29	55	15
Total No. bait stations	158	426	268
Total No. grid cells	5	24	23

Table 2. Ant species collected at the three protected areas. X indicates the presence of a species, Abr = Abbreviation. CS = Cryptic species, DD = Dominant Dolichoderinae, HCS = Hot climate specialist, SC = Subordinate Camponotini, OPP = Opportunistic, TCS = Tropical Climate Specialists, SP = Specialized Predators, CCS = Cold Climate Specialists, and GM = Generalized Myrmicinae. Functional groups after Andersen (1997). Foraging habits are based on generic level habits (DiGirolamo & Fox 2006; Brown 2000). * = Alien invasive species. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, KBR = Kogelberg Biosphere Reserve, Inv = Invaded, and Uninv = Uninvaded.

Species	**Abr.**	**Foraging habits**	**Functional group**	**Nature Reserve**					
				HNR		**JNR**		**KBR**	
				Inv	**Uninv**	**Inv**	**Uninv**	**Inv**	**Uninv**
Dolichoderinae									
Linepithema humile Mayr*	Lhum	Epigaeic	DD	X		X		X	
Formicinae									
Anoplolepis custodiens Smith	Acus	Epigaeic	HCS	X	X		X		X
Anoplolepis sp. 3	Ano3	Epigaeic	HCS		X		X		
Anoplolepis steingroeveri Forel	Aste	Epigaeic	HCS		X		X		
Camponotus niveosetosus Mayr	Cniv	Epigaeic	SC			X			
Camponotus sp. 1	Cam1	Epigaeic	SC				X	X	X
Lepisiota sp. 1	Lep1	Hypogaeic	OPP	X	X		X		X
Lepisiota sp. 3	Lep3	Hypogaeic	OPP				X		

Species	Abr.	Foraging habits	Functional group	Nature Reserve					
				HNR		JNR		KBR	
				Inv	Uninv	Inv	Uninv	Inv	Uninv
Lepisiota sp. 4	Lep4	Hypogaeic	OPP				X		
Lepisiota sp. 5	Lep5	Hypogaeic	OPP				X		
Plagiolepis sp. 1	Pla1	Hypogaeic	CS			X	X		
Plagiolepis sp. 2	Pla2	Hypogaeic	CS			X	X		
Myrmicinae									
Crematogaster sp. 2	Cre2	Arboreal	GM					X	
Crematogaster sp. 3	Cre3	Arboreal	GM			X	X		X
Leptothorax sp. 1	Lep1	Hypogaeic	CCS				X		
Meranoplus peringueyi Emery	Mper	Epigaeic	TCS	X	X	X	X	X	X
Monomorium havilandi Forel	Mhav	Epigaeic	GM				X		
Monomorium sp. 1	Mon1	Epigaeic	GM				X		
Monomorium sp. 8	Mon8	Epigaeic	GM	X	X	X		X	X
Myrmicaria nigra Mayr	Mnig	Epigaeic	TCS		X				X
Ocymyrmex barbiger Emery	Obar	Epigaeic	HCS	X	X	X	X		
Pheidole capensis Mayr	Pcap	Epigaeic	GM		X	X	X	X	X
Pheidole sp. 5	Phe5	Epigaeic	GM			X	X		
Pheidole sp. 1	Phe1	Epigaeic	GM						X

Species	Abr.	Foraging habits	Functional group	Nature Reserve					
				HNR		JNR		KBR	
				Inv	Uninv	Inv	Uninv	Inv	Uninv
Pheidole sp. 3	Phe3	Epigaeic	GM				X		
Tetramorium quadrispinosum Emery	Tqua	Epigaeic	OPP	X	X	X	X	X	X
Tetramorium sp. 1	Tet1	Epigaeic	OPP					X	X
Ponerinea									
Pachycondyla pumicosa Forel	Ppum	Epigaeic	SP						X
Species richness				**8**	**10**	**11**	**20**	**7**	**12**

Table 3. Generalized Linear Model results for differences in mean abundances of each ant species at three protected areas and at bait stations invaded or uninvaded by the Argentine ant (status) (see Table 4 for Mean ± S.E.). See Table 1 for species abbreviations. Asterisks indicate species only collected at invaded or uninvaded sites, and those collected at both invaded and uninvaded sites but only at one reserve. Scaled deviance = 1.0.

Species	**Goodness of fit**		**Type III Test**					
	Deviance	**df**	**Reserve**			**Status (Invaded/Uninvaded)**		
			df	X^2	P <	df	X^2	P <
*Lhum**	96.29	849	2	133.31	0.001	_	_	_
Pcap	30.56	691	1	23.47	0.001	1	121.6	0.001
Tqua	9.65	848	2	124.28	0.001	1	1.17	0.28
Cre3	4.66	691	1	28.97	0.001	1	1.37	0.24
*Mon8**	5.32	266	_	_	_	1	0.33	0.56
*Aste**	13.36	582	1	18.45	0.001	_	_	_
*Acus**	7.12	849	2	34.71	0.001	_	_	_
*Phe5**	4.98	424	_	_	_	1	41.86	0.001
Mper	10.13	691	1	33.09	0.001	1	0.01	0.89
*Ano3**	5.16	582	1	0.21	0.64	_	_	_

Table 4. Mean (± S.E.) ant species abundances at bait stations at three protected areas at invaded and uninvaded bait stations. See Table 1 for abbreviations. _ = species not collected for that reserve/status, √ = species only collected from that reserve or status, and different letters indicate significant differences at $p < 0.05$ between reserves or status. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, and KBR = Kogelberg Biosphere Reserve.

Species		**Reserve**			**Status**	
		HNR	**JNR**	**KBR**	**Invaded**	**Uninvaded**
Lhum		64.72 ± 0.09 [a]	40.29 ± 0.07 [b]	6.57 ± 0.23 [c]	√	_
Pcap		_	0.67 ± 0.55 [a]	1.52 ± 0.55 [b]	0.10± 1.08 [a]	9.95 ± 0.08 [b]
Tqua		0.35 ± 0.41 [a]	0.94 ± 0.16 [a]	4.47 ± 0.09 [b]	1.24 ± 0.17	1.04 ± 0.17 n.s.
Cre3		_	0.28 ± 0.19 [a]	0.94 ± 0.14 [b]	0.44 ± 0.20	0.59 ± 0.14 n.s.
Mon8		_	_	√	1.06 ± 0.23	0.89 ± 0.18 n.s.
Aste		1.03 ± 0.29 [a]	3.18 ± 0.09 [b]	_	_	√
Acus		2.16 ± 0.14 [a]	0.79 ± 0.15 [b]	0.53 ± 0.22 [b]	_	√
Phe5		_	√	_	0.02 ± 1.11 [a]	0.96 ± 0.14 [b]
Mper		_	1.76 ± 0.12 [a]	0.33 ± 0.34 [b]	0.77 ± 0.23	0.75 ± 0.19 n.s.
Ano3		0.58 ± 0.25	0.50 ± 0.16 n.s.	_	_	√
Overall mean	**Invaded**	17.94 ± 0.08	12.21 ± 0.04	4.23 ± 0.08		
	Uninvaded	2.95 ± 0.32	1.96 ± 0.09	2.92 ± 0.07		

Table 5. Variance ratios (VR) and C-scores of multispecies associations and abundance covariation, N = number of bait stations, W = test statistic of variance ratio with a chi-square distribution (Schluter 1984). * = Significant at P < 0.05, n.s. = non-significant at P >= 0.05. SES = Standardized Effect Size. The Argentine ant was included in the analysis. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, and KBR = Kogelberg Biosphere Reserve.

Reserve	**N**	**VR**	**W**	**C-Score**			**p(observed > = expected)**
				Observed	Expected	SES	
SPECIES ASSOCIATION							
HNR							
Uninvaded	44	0.62	27.28 n.s.	12.07	10.67	2.03	p < 0.001
Invaded	114	1.25	142.23*	1.71	1.89	-1.69	n.s.
JNR							
Uninvaded	265	0.77	205.37*	70.87	64.03	4.40	p < 0.001
Invaded	161	1.21	194.52*	11.60	13.65	-1.48	n.s.
KBR							
Uninvaded	170	0.89	151.69 n.s.	100.29	89.26	2.67	p < 0.001
Invaded	98	1.25	122.86*	22.28	28.15	-1.75	n.s.
ABUNDANCE COVARIATION							
HNR							
Uninvaded	44	0.88	39.72 n.s.				
Invaded	114	0.69	78.66 n.s.				
JNR							
Uninvaded	265	1.22	323.03*				
Invaded	161	1.01	162.08 n.s.				
KBR							
Uninvaded	170	2.66	451.5*				
Invaded	98	2.04	200.19*				

Table 6. Relationships between abundances of the Argentine ant and native ant species (at bait stations) at three protected areas, indicated by Spearman' rank correlation coefficients (r). O = number of bait stations occupied by species; * = Significant at P < 0.05; _ = species not collected in nature reserve. Total number of bait stations in parentheses. Correlations calculated only for species with a minimum occupancy of 10. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, and KBR = Kogelberg Biosphere Reserve.

	HNR (158)		**JNR** (426)		**KBR** (268)	
Species	**O**	**r**	**O**	**r**	**O**	**r**
Linepithema humile	114		161		98	
Anoplolepis custodiens	8	_	17	-0.153*	4	_
Anoplolepis sp. 3	2	_	3	_	0	_
Anoplolepis steingroeveri	5	_	52	-0.279*	0	_
Camponotus niveosetousus	0	_	1	_	0	_
Camponotus sp. 1	0	_	1	_	18	0.069
Lepisiota sp. 1	7	_	8	_	10	-0.144*
Lepisiota sp. 3	0	_	1	_	0	_
Lepisiota sp. 4	0	_	1	_	0	_
Lepisiota sp. 5	0	_	4	_	0	_
Plagiolepis sp. 1	0	_	8	_	0	_
Plagiolepis sp. 2	0	_	4	_	0	_
Crematogaster sp. 2	0	_	0	_	2	_
Crematogaster sp. 3	0	_	39	0.345*	3	_
Leptothorax sp. 1	0	_	3	_	0	_
Meranoplus peringueyi	3	_	18	-0.005	8	_
Monomorium havilandi	0	_	4	_	0	_
Monomorium sp. 1	0	_	10	-0.036	0	_
Monomorium sp. 8	2	_	1	_	24	-0.095
Myrmicaria nigra	1	_	0	_	2	_
Ocymyrmex barbiger	11	-0.345*	7	_	0	_

	HNR (158)		**JNR** (426)		**KBR** (268)	
Species	**O**	**r**	**O**	**r**	**O**	**r**
Pheidole capensis	1	_	27	-0.161*	56	-0.352*
Pheidole sp. 5	0	_	10	-0.096*	0	_
Pheidole sp. 1	0	_	0	_	5	_
Pheidole sp. 2	2	_	0	_	0	_
Pheidole sp. 3	0	_	5	_	0	_
Tetramorium quadrispinosum	7	_	26	-0.115*	59	0.117
Tetramorium sp. 1	0	_	0	_	2	_
Pachycondyla pumicosa	0	_	0	_	4	_

Table 7. Mean (± S.E.) ant *βeta* diversity for invaded and uninvaded bait stations at three Protected Areas, and for the entire Protected Area (overall). Different letters indicate significant difference between means at $p < 0.05$. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, and KBR = Kogelberg Biosphere Reserve.

Reserve	**Invaded**	**Uninvaded**	**Overall**
HNR	0.0005 ± 0.001 [a]	0.80 ± 0.005 [b]	0.07 ± 0.005
JNR	0.001 ± 0.002 [a]	0.81 ±0.002 [b]	0.38 ± 0.003
KBR	0.03 ± 0.005 [a]	0.68 ± 0.005 [b]	0.40 ± 0.004
Total	0.008 ± 0.002 [a]	0.77 ± 0.002 [b]	0.33 ± 0.002

Table 8. Associations between the Argentine ant and native ant species at three protected areas based on results from the current study. Inferences about association were made based on the content of the literature references, i.e. references did not directly address interactions between the Argentine ant and native ant species contained in this table.

Ant species	Evidence	Literature information (based on generic level classification)	References
Associations found in this study			
Positive			
Tetramorium quadrispinosum	Figs. 5 & 6	Subdominant to the Argentine ant.	Addison & Samways 2000
Meranoplus peringueyi	Figs. 5 & 6	Occurs in areas where the Argentine ant is not dominant.	Andersen 2000
Monomorium sp. 8	Figs. 5 & 6	Uses chemical secretions to repel attacks from the Argentine ant.	Holway 1999
Crematogaster sp. 2	Figs. 5 & 6	Arboreal, does not interact directly with the epigaeic the Argentine ant.	Brown 2000
Crematogaster sp. 3	Figs. 5 & 6	Arboreal, does not interact directly with the epigaeic the Argentine ant.	Brown 2000
Negative			
Pheidole capensis	Table 4; Figs. 4, 5, & 6	Has similar resource requirements to the Argentine ant.	Reimer 1994

Ant species	Evidence	Literature information (based on generic level classification)	References
Associations found in this study			
negative			
Pheidole sp. 5	Table 4; Figs. 4, 5, & 6	Has similar resource requirements to the Argentine ant.	Reimer 1994
Anaplolepis steingroeveri	Table 4; Figs. 4, 5, & 6	Has morphological, physiological and behavioural features that reduces its interactions with the Argentine ant.	Hoffmann & Andersen 2003
A. custodiens	Table 4; Figs. 4, 5, & 6	Has morphological, physiological and behavioural features that reduces its interactions with the Argentine ant.	Hoffmann & Andersen 2003
Anaplolepis sp. 3	Table 4; Figs. 4, 5, & 6	Has morphological, physiological and behavioural features that reduces its interactions with the Argentine ant.	Hoffmann & Andersen 2003
Neutral			
Monomorium sp. 1	Table 6	Uses chemical secretions to repel attacks from the Argentine ant.	Holway 1999
Camponotus sp. 1	Fig. 4D	Behaviourally submissive to the Argentine ant.	Hoffmann & Andersen 2003

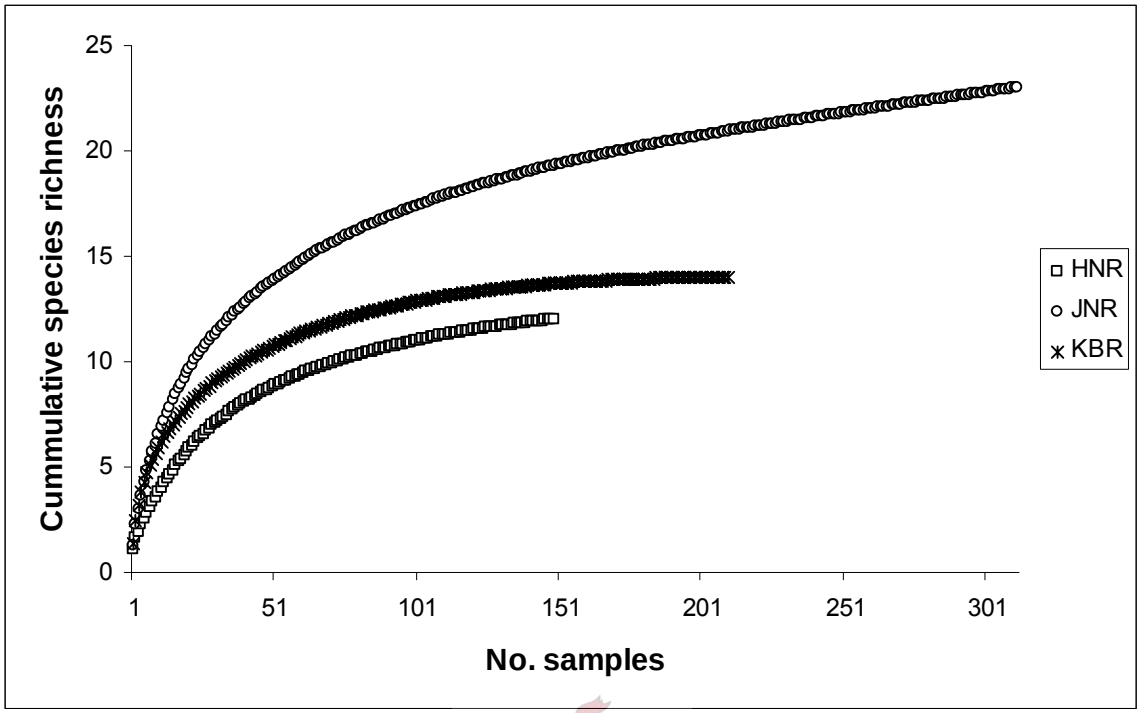


Fig. 1. Rarefaction curves for three protected areas. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, and KBR = Kogelberg Biosphere Reserve

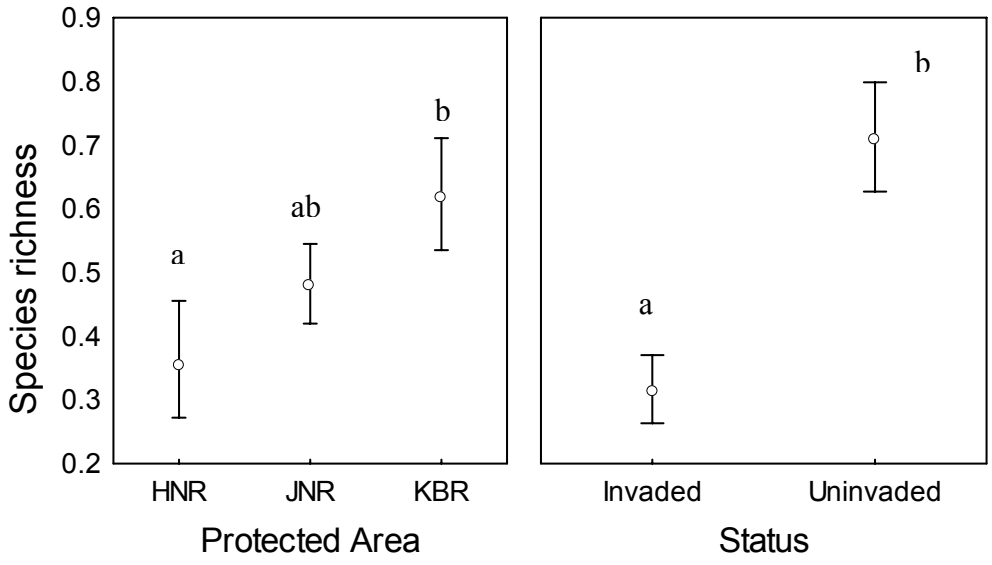


Fig. 2. Predicted mean (± S.E.) number of ant species at bait stations based on GLZ analysis with Protected Area and invasion-status as factors. The Argentine ant was excluded from the analysis. Different letters indicate significant difference between means at $p < 0.05$. See Table 1 for total number of bait stations in each reserve. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, KBR = Kogelberg Biosphere Reserve.

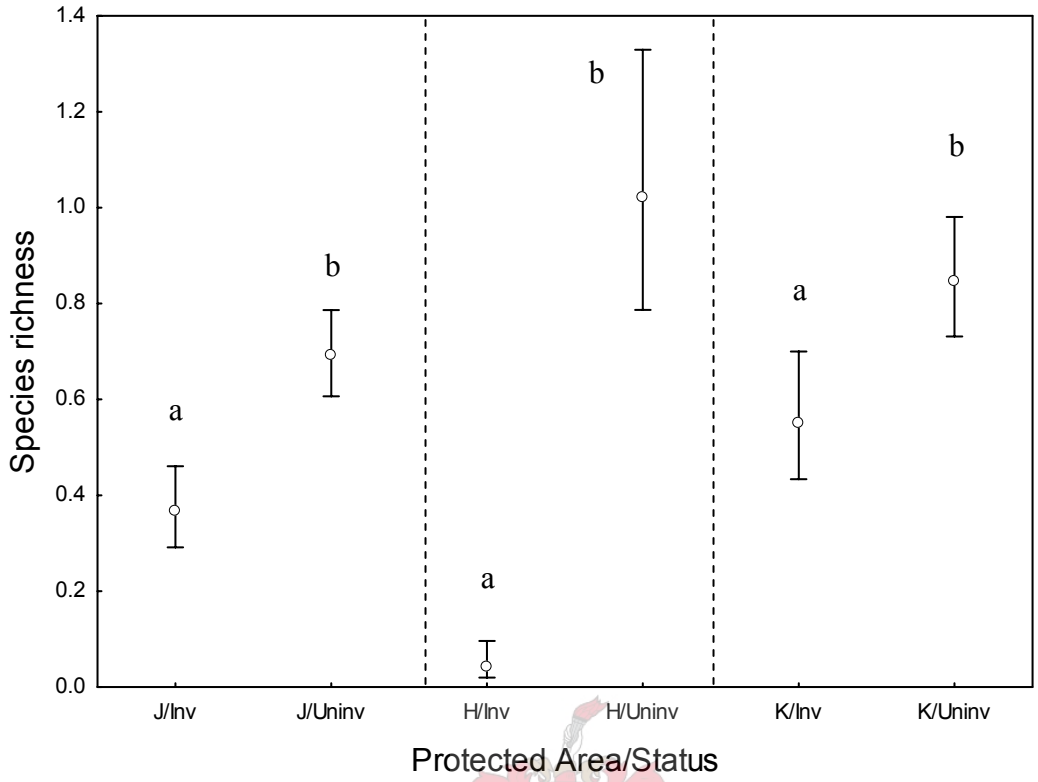


Fig. 3. Predicted mean (± S.E.) number of ant species at bait stations in three Protected Areas. The Argentine ant was excluded from the analysis. Different letters indicate significant difference between means at $p < 0.05$. See Table 1 for total number of bait stations in each reserve. H/Inv = Helderberg Nature Reserve/invaded, H/Uninv = Helderberg Nature Reserve/uninvaded, J/Inv = Jonkershoek Nature Reserve/invaded, J/Uninv = Jonkershoek Nature Reserve/uninvaded, K/Inv = Kogelberg Biosphere Reserve/invaded, K/Uninv = Kogelberg Biosphere Reserve/uninvaded.

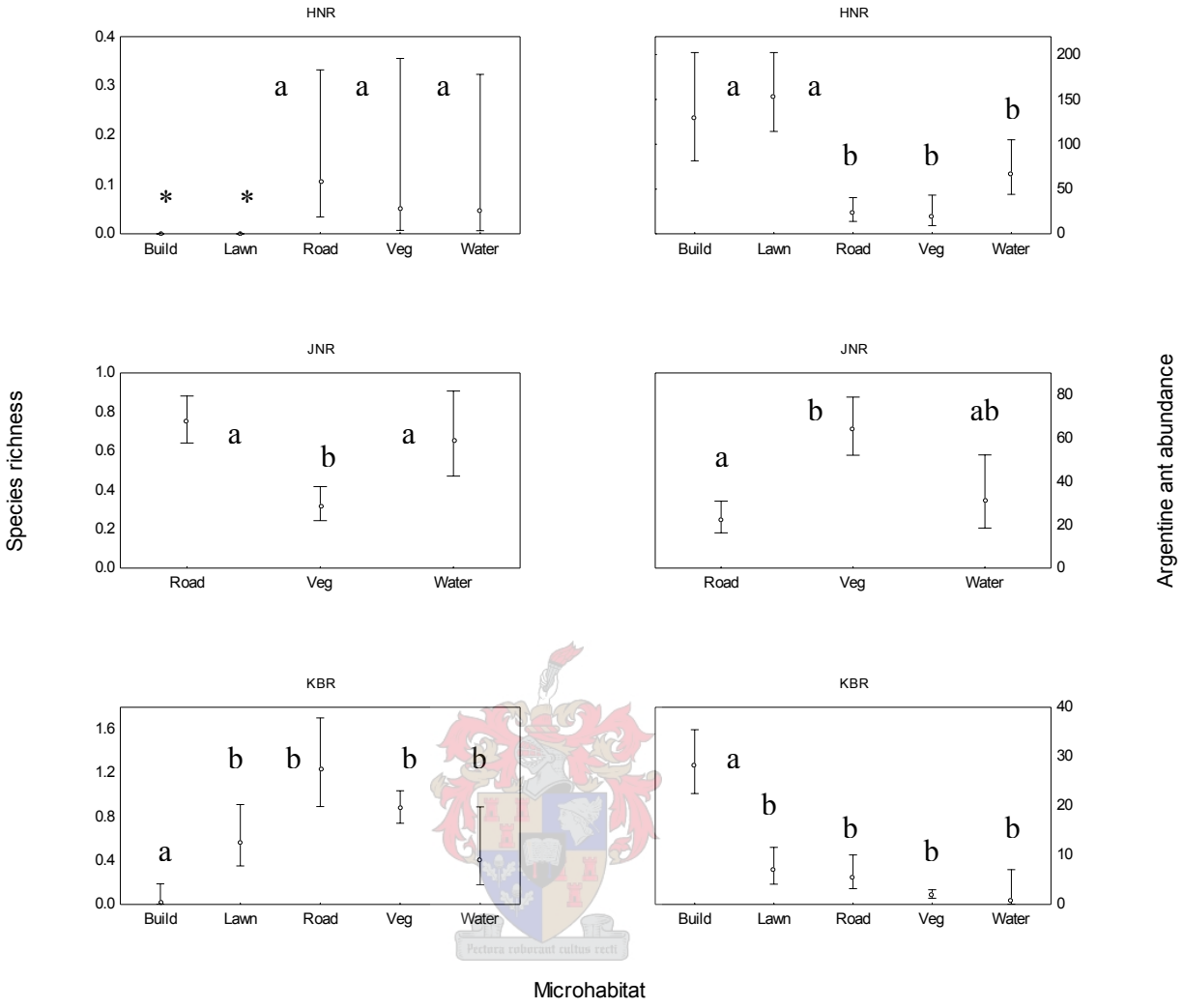
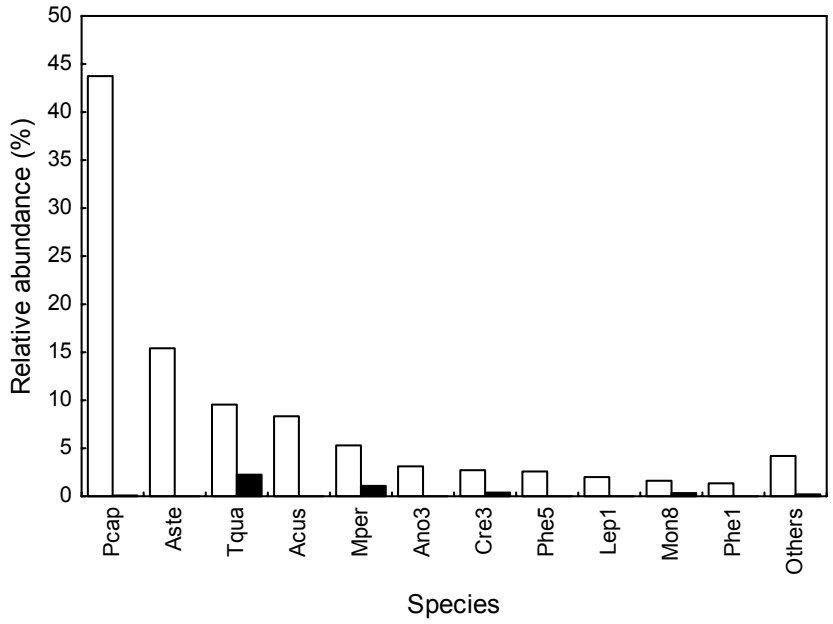


Fig. 4. Mean (± S.E.) ant species richness and Argentine ant abundances at invaded bait stations at different microhabitats in three Protected Areas. * = the Argentine ant was the only ant species collected at these microhabitats. The Argentine ant was excluded from the analysis for all three protected areas. Different letters indicate significant differences between means at $p < 0.05$. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, KBR = Kogelberg Biosphere Reserve, Build = Buildings, Veg = Vegetation, and Water = Waterbodies. Note differences in Y-axis scales.

A.


Relative abundance (%)
50
45
40
35
30
25
20
15
10
5
0
Pcap
Aste
Tqua
Acus
Mper
Ano3
Cre3
Phe5
Lep1
Mon8
Phe1
Others
Species

B.

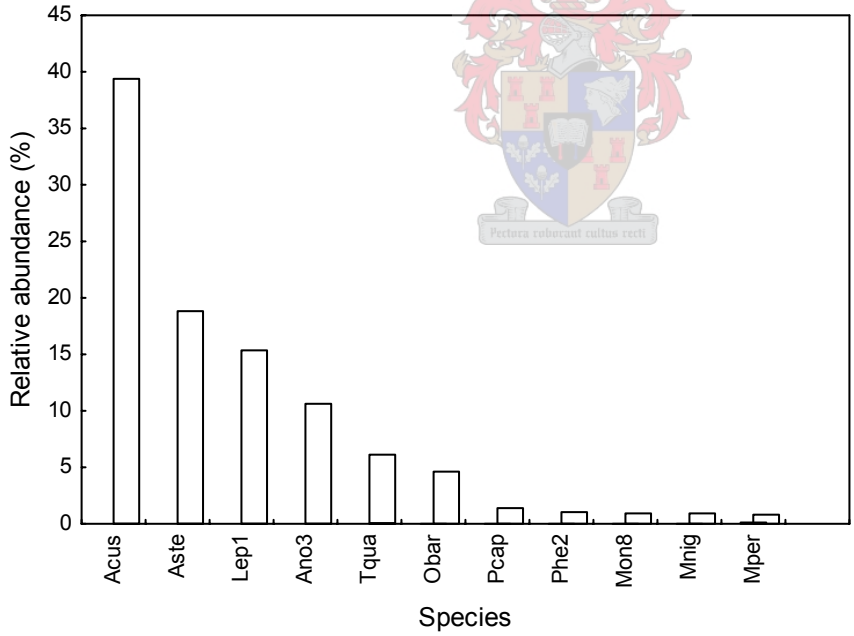
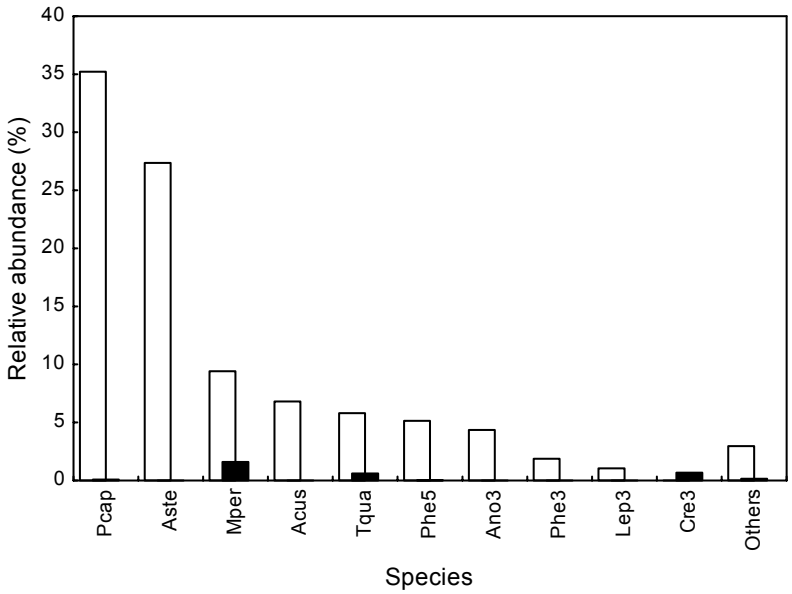

Relative abundance (%)
45
40
35
30
25
20
15
10
5
0
Acus
Aste
Lep1
Ano3
Tqua
Obar
Pcap
Phe2
Mon8
Mnig
Mper
Species

Fig. 5 A, B.

C.



D.

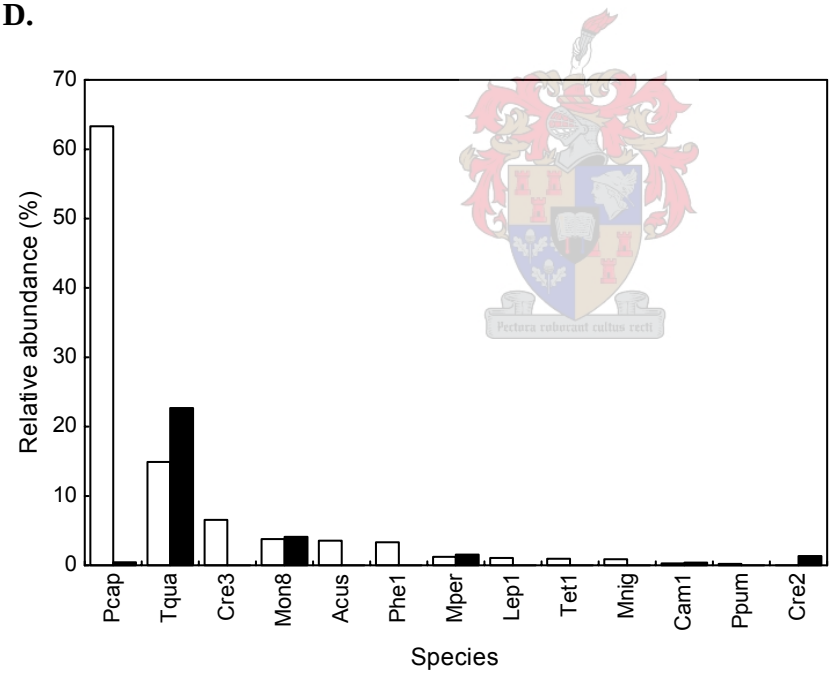
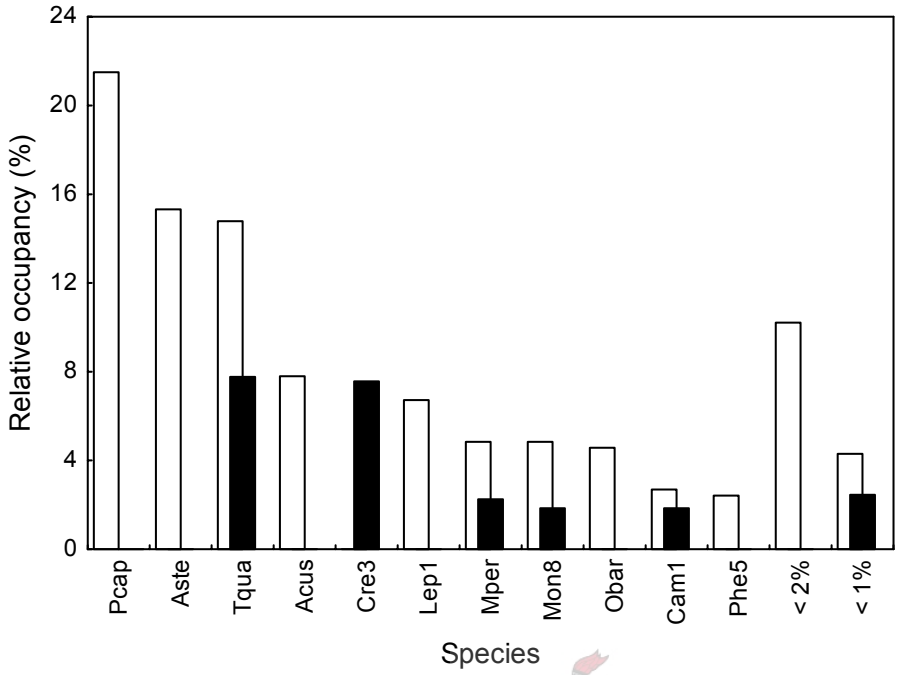


Fig. 5. Relative native ant species abundances at invaded (shaded bars) and uninvaded (open bars) bait stations at A. all three protected areas combined, B. Helderberg Nature Reserve, C. Jonkershoek Nature Reserve, and D. Kogelberg Biospere Reserve. Argentine ant abundances are 69.5 %, 95.6 %, 99.8 % and 96.9 % for A, B, C, and D respectively. See Table 1 for abbreviations.

A.


Relative occupancy (%)
0
4
8
12
16
20
24
Pcap
Aste
Tqua
Acus
Cre3
Lep1
Mper
Mon8
Obar
Cam1
Phe5
< 2%
< 1%
Species

B.

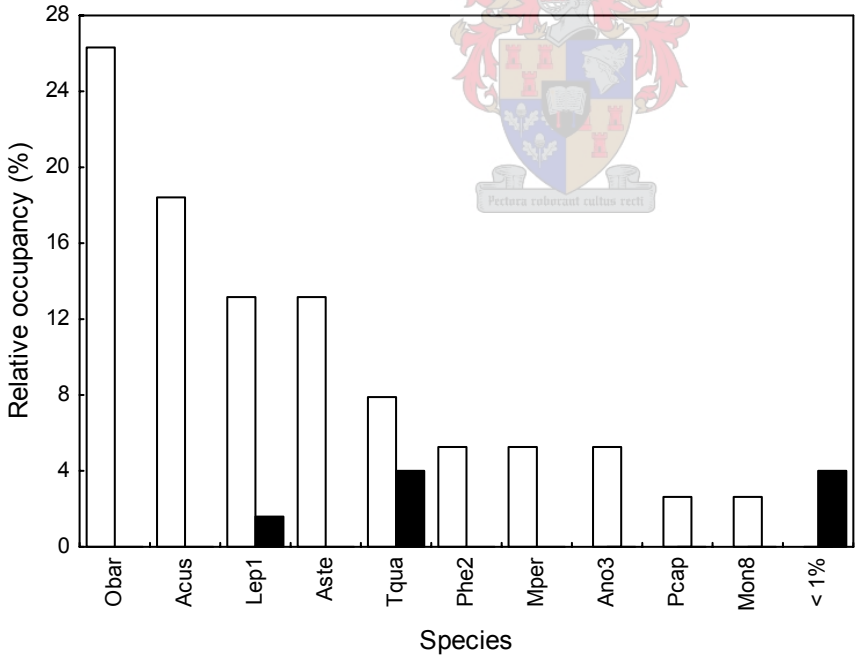
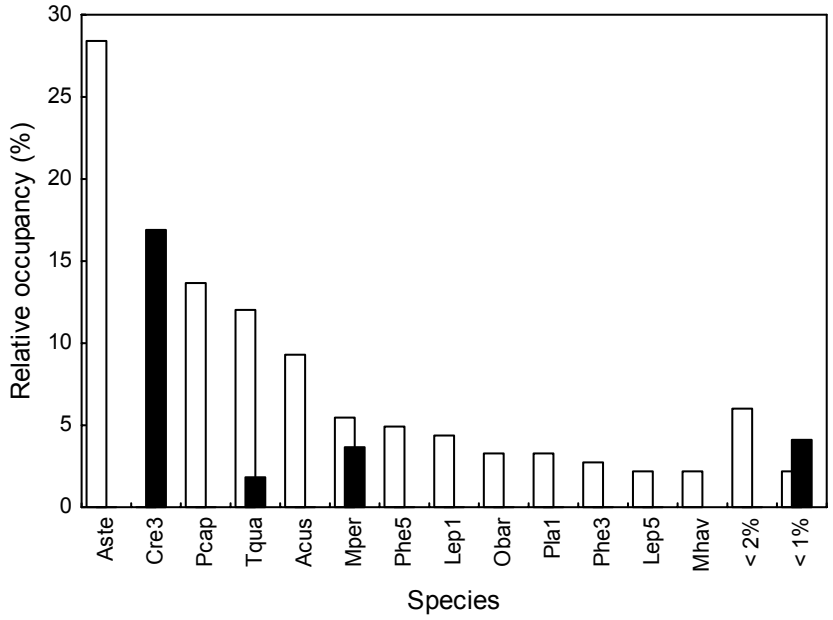

Relative occupancy (%)
0
4
8
12
16
20
24
28
Obar
Acus
Lep1
Aste
Tqua
Phe2
Mper
Ano3
Pcap
Mon8
< 1%
Species

Fig. 6 A, B.

C.



D.

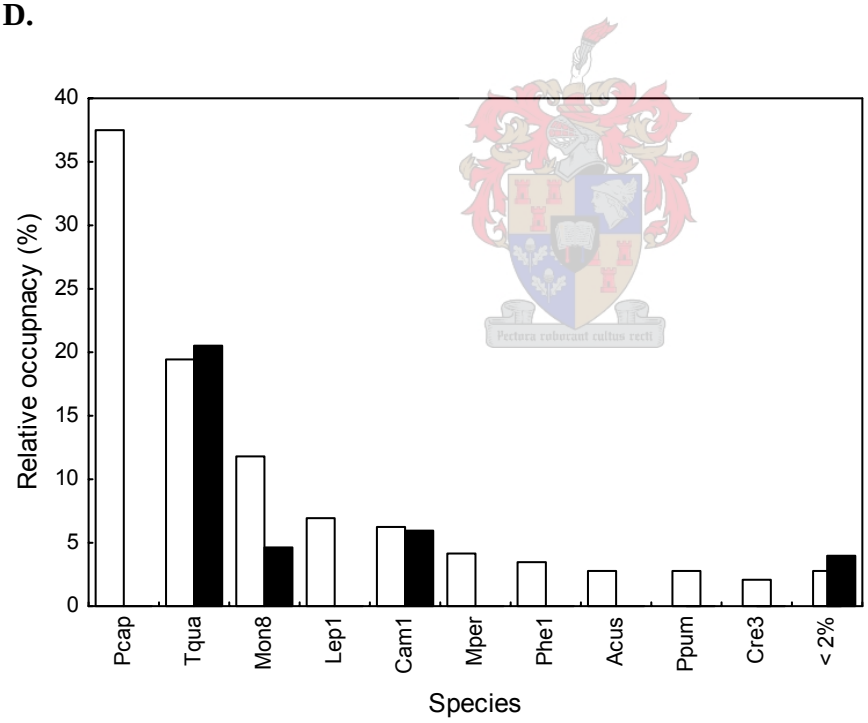
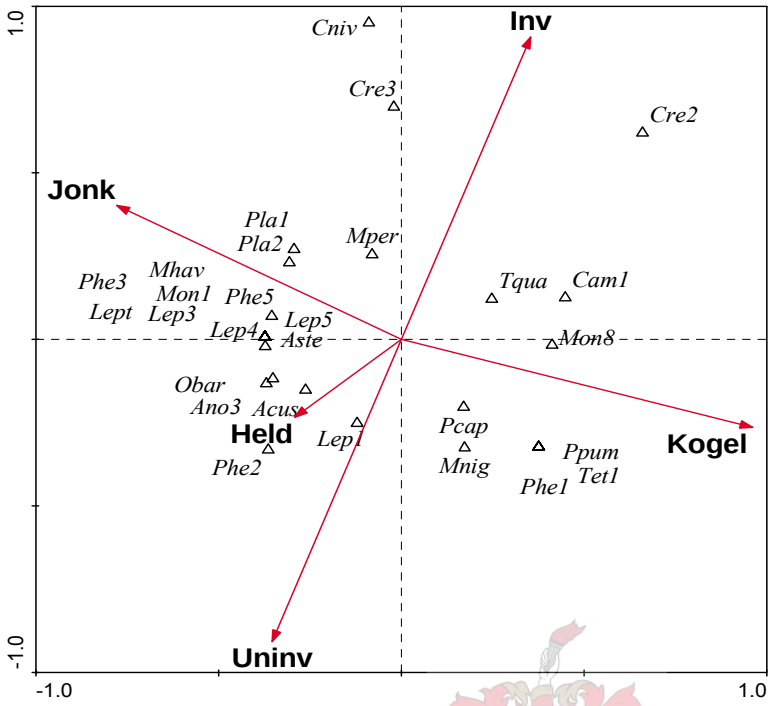


Fig. 6. Relative native ant species occupancies at invaded (shaded bars) and uninvaded (open bars) bait stations at **A.** all three protected areas combined, **B.** Helderberg Nature Reserve, **C.** Jonkershoek Nature Reserve, and **D.** Kogelberg Biosphere Reserve. Argentine ant occupancies are 76.3 %, 90.4 %, 73.5 % and 64.9 % for A, B, C, and D respectively. See Table 1 for abbreviations.

A.


Inv
Jonk
Held
Kogel
Uninv
Cniv
Cre3
Cre2
Pla1
Pla2
Mper
Phe3
Mhav
Mon1
Phe5
Lept
Lep3
Lep5
Lep4
Aste
Tqua
Cam1
Mon8
Obar
Ano3
Acus
Lep1
Phe2
Pcap
Mnig
Ppum
Tet1
Phe1
1.0
-1.0
-1.0
1.0

B.

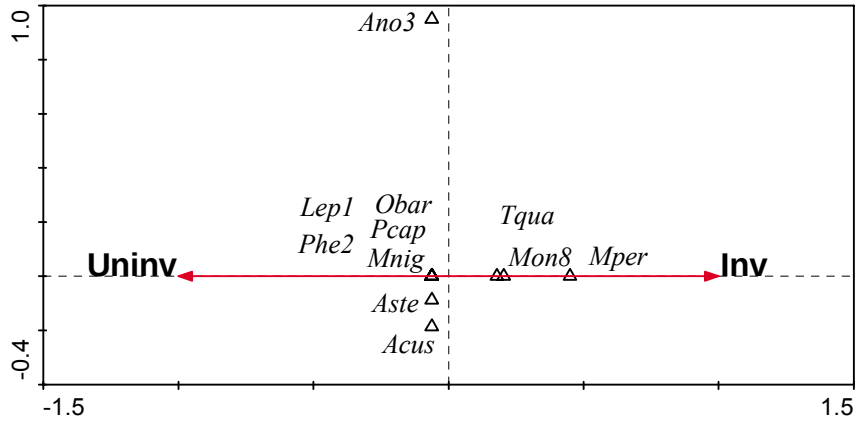
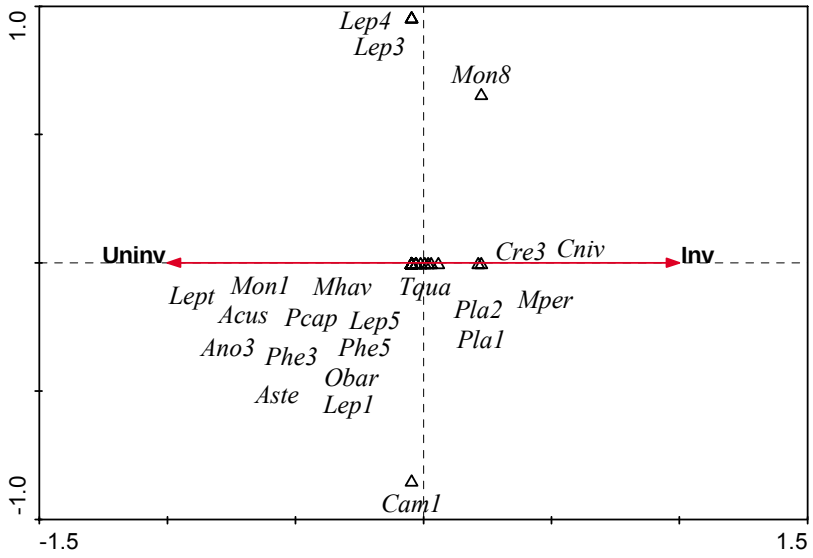

Ano3
Lep1
Obar
Pcap
Phe2
Mnig
Tqua
Mon8
Mper
Uninv
Inv
Aste
Acus
1.0
-0.4
-1.5
1.5

Fig. 7 A, B.

C.



D.

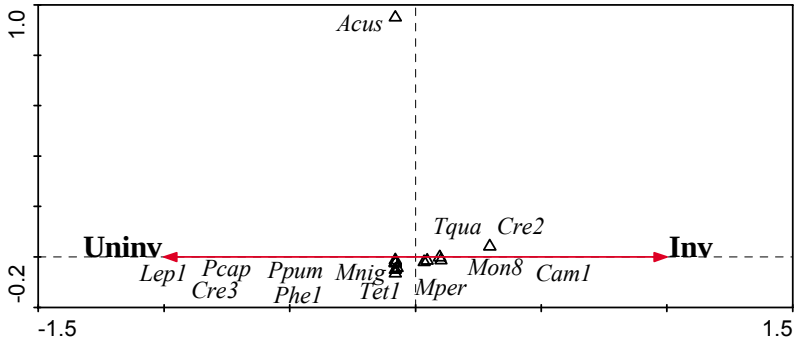
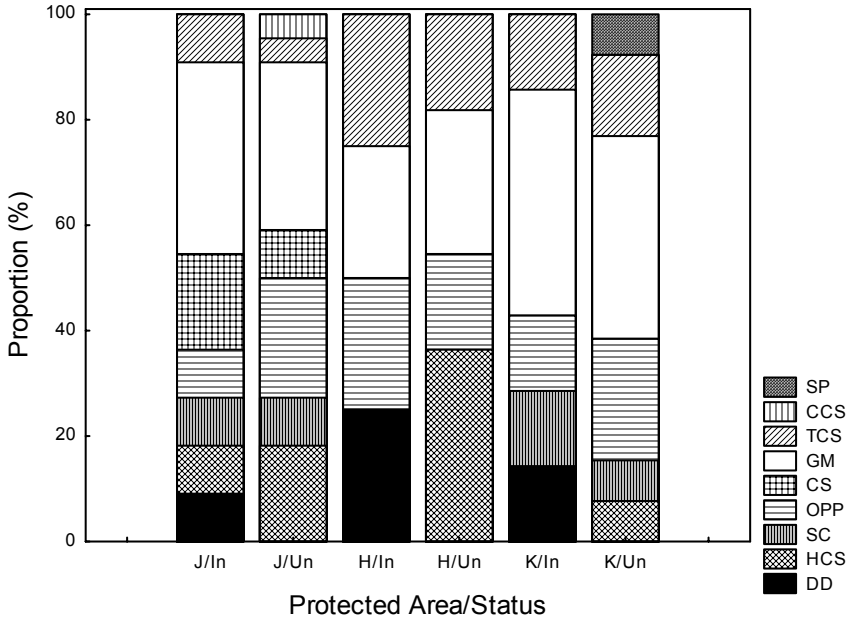


Fig. 7. Ordinations of ant assemblage structure at invaded and uninvaded bait stations for **A.** data combined for all three protected areas, **B.** Helderberg Nature Reserve (Held), **C.** Jonkershoek Nature Reserve (Jonk) and **D.** Kogelberg Biosphere Reserve (Kogel). Ordination plots are based on species abundance data. Inv = Invaded, and Uninv = Uninvaded bait stations.

A.



B.

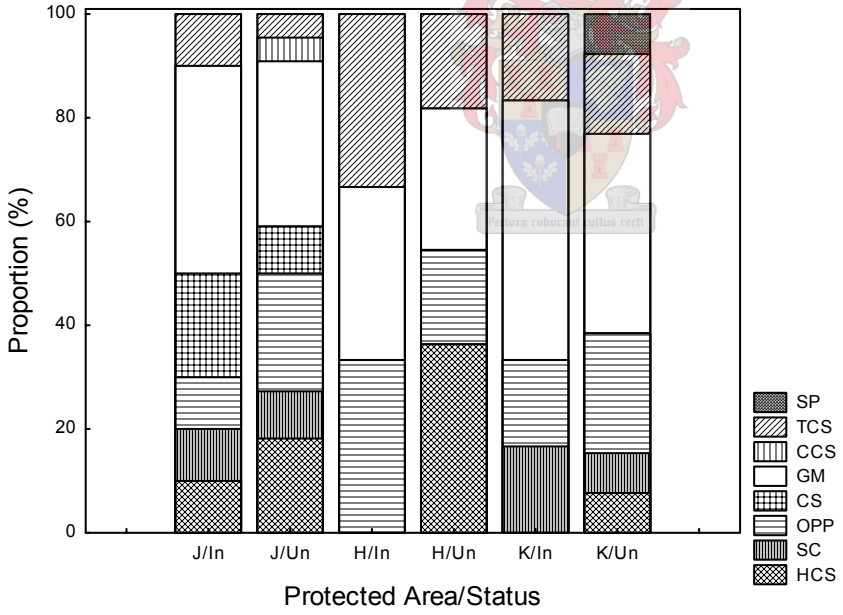
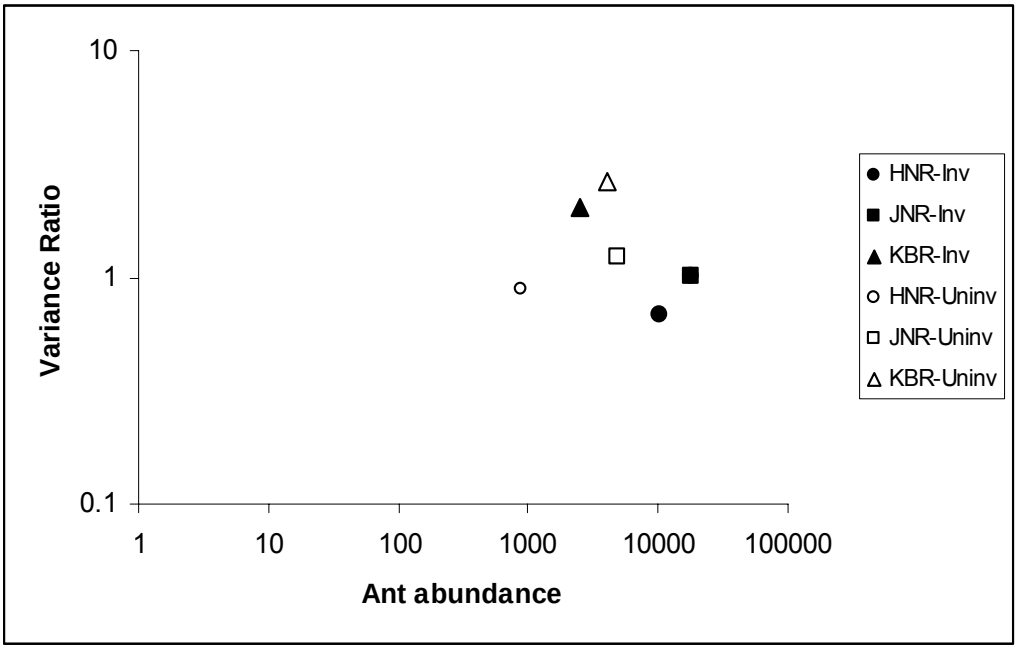


Fig. 8. The proportion of ant species in functional groups at invaded (In) and uninvaded (Un) bait stations at three Protected Areas, **A.** including DD (Argentine ant) and **B.** excluding DD at invaded bait stations. J = Jonkershoek Nature Reserve, H = Helderberg Nature Reserve, and K = Kogelberg Biosphere Reserve. Refer to Table 1 for functional group abbreviations.

A.



B.

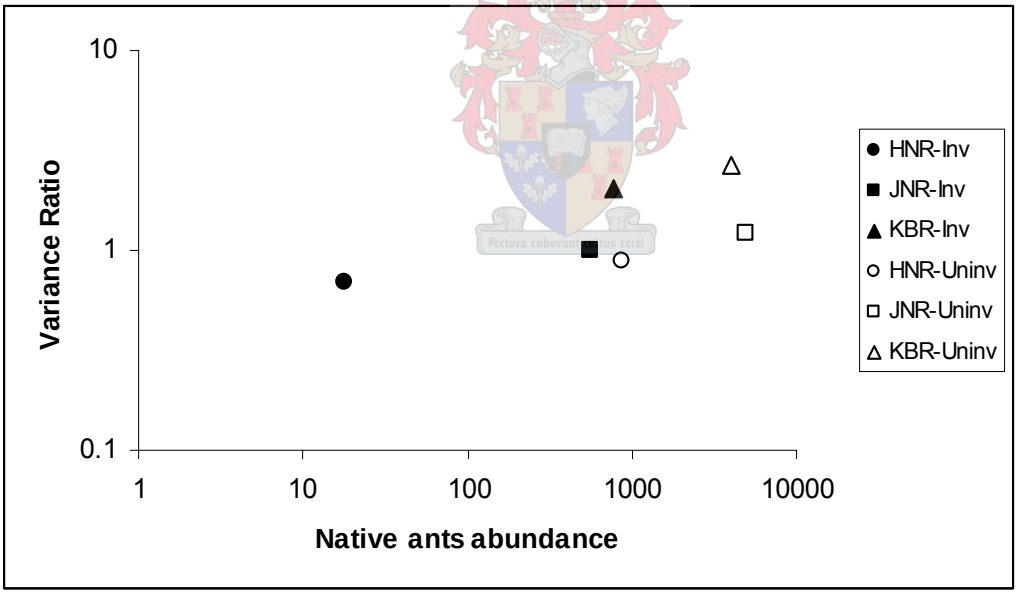


Fig. 9. Relationship between variance ratio and ant abundance at invaded and uninvaded bait stations at HNR, JNR, and KBR. **A.** Including Argentine ant abundance, and **B.** excluding Argentine ant abundance. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, KBR = Kogelberg Biosphere Reserve, Inv = Invaded, and Uninv = Uninvaded bait stations. Ant abundance includes both native ants and the Argentine ant. A logarithmic scale was used for both X- and Y-axes.

CHAPTER 3

Distribution and habitat preferences of the Argentine ant in protected areas in South Africa

INTRODUCTION

Over the past decades, the Argentine ant (*Linepithema humile* Mayr) (Hymenoptera: Formicidae) has successfully invaded almost all regions with Mediterranean and Subtropical climates globally, i.e. six continents and many oceanic islands (Suarez *et al*. 2001). Although it is native to Argentina, its current global distribution range continues to increase (Passera 1994). The Argentine ant is well established in most of its invaded ranges, and has become an urban as well as an agricultural pest in many countries, including South Africa (Markin 1970; Prins *et al*. 1990; Addison & Samways 2000; Vega & Rust 2001).

The current introduced range of the Argentine ant is most likely to continue to increase with the increase in global international trade (Keane & Crawley 2002). As humans travel around the globe, they move species beyond their native ranges, both deliberately and accidentally (Vitousek *et al*. 1997; McGlynn 1999). For example, the most common pathway of exotic species into the United States is via unintentional importation through international trade (Jenkins 1996). About 115 ant species, including the invasive *Pheidole megacephala*, were introduced into New Zealand via different trade pathways over a period of 50 years (Ward *et al*. 2006). Although the greatest transport of the Argentine ant across the globe is human-mediation (Hölldobler & Wilson 1990), this species can also spread by budding of the nest at a local scale.

Although the Argentine ant is a typical tramp species (i.e. usually associated with human activities (Passera 1994)), it has been shown to invade natural habitats, although its penetration into these undisturbed habitats is usually limited (Holway 1995). For example, in South Africa, the Argentine ant has been found in undisturbed habitats such as Kogelberg Biosphere Reserve (Bond & Slingsby 1984; Christian 2001), Jonkershoek Nature Reserve (De Kock 1990; Witt 1993) and Helderberg Nature Reserve (Boonzaaier 2006). Similarly, the Argentine ant has also been shown to invade natural habitats in northern California, e.g. Jasper Ridge Biological Preserve (Human *et al*. 1998).

Nonetheless, the Argentine ant has been shown to be strongly associated with particular habitat qualities, especially those associated with human activities (Passera 1994). For example, in Spain (Doñana National Park) Carpintero *et al*. (2003) found the Argentine ant in close proximity to inhabited houses. These houses were situated in a variety of habitat types,

including xerophytic scrubland, dense pine plantations and grasses (Carpintero *et al*. 2003). Abiotic factors such as moisture availability (both in urban and natural areas) play an important role in the extent to which the Argentine ant invades natural areas (Human *et al*. 1998; Holway *et al*. 2002; DiGirolamo & Fox 2006). Menke and Holway (2006) demonstrated that the abundance of the Argentine ant increased or decreased dramatically in response to the availability or lack of soil moisture in California. Spread of Argentine ants has also been shown to be facilitated by rivers and floodplains (Ward 1987; Holway 1998a). The distribution and spread of the Argentine ant may also be limited by biotic resistance, i.e. its interaction with native ants. As proposed by Elton (1958), the biotic resistance hypothesis predicts that areas with high species richness will be less likely to experience biological invasion than areas with lower species richness. Previous studies that have also found some evidence of biotic resistance by native species include Ward (1987), Crawley *et al*. (1999) and Walters and Mackay (2005).

It is assumed that the Argentine ant was introduced into Southern Africa during the Anglo Boer war, more than a century ago. The first record of the Argentine ant in South Africa was in 1901 in the area of Stellenbosch (Prins *et al*. 1990). Since then, this species has become established in urban, agricultural (Addison & Samways 2000) and protected areas (Fynbos) (Bond & Slingsby 1984; De Kock 1990; Witt 1993) in the Western Cape Province. Although the Argentine ant has been in the country (South Africa) for more than 100 years and is widespread in urban areas, very little is known about the extent of invasion and distribution range inside protected areas. Factors influencing the spread (such as microhabitat preferences and altitude) of the Argentine ant inside these areas are also poorly understood.

The aim of this study was thus to quantify the invasion of protected areas in the Western Cape Province, South Africa by the Argentine ant and to determine if the invasion and spread of this species is associated with particular habitat quality characteristics. Therefore, the following hypothesis regarding habitat preferences of the Argentine ant were tested: (1) The Argentine ant is predominantly associated with human activities inside protected areas, i.e. buildings, roadverges and lawns. (2) The distribution of the Argentine ant in protected areas is associated with permanent water sources, such as along the edges of rivers, dams and lakes. (3) The abundance and occupancy of the Argentine ant are altitude independent.

MATERIALS AND METHOD

Study sites

This study was conducted in three protected areas in the Boland region of the south Western Cape Province, South Africa (i.e. Jonkershoek Nature Reserve (JNR), Helderberg Nature Reserve (HNR) and Kogelberg Biosphere Reserve (KBR)). The southern part of the Western Cape Province has a Mediterranean-type climate, with winter rainfall (June-August) and a warm, dry summer (October-March). The reserves in the study are dominated by Fynbos vegetation, i.e. an evergreen, narrow-leaved sclerophyllous shrubland growing on young, shallow, nutrient poor soils (Witch *et al*. 1969; Moll & Jarman 1984; Schlettwein & Giliomee 1987; Cowling & Holmes 1992). In addition, these protected areas contain other habitat types: mountain, riparian, forest and lowland vegetation (Boucher 1978; Le Maitre *et al*. 1996). Each reserve encompasses perennial streams supporting a continuous river stretching across the reserve (see Fig. 3). These reserves include recreational areas, such as picnic sites and hiking trails, and they attract a large number of people on a daily basis, especially during the summer period.

Helderberg Nature Reserve (34°03' S, 18°52'E) is situated outside the town of Somerset West, and is dominated by Mesic Mountain Fynbos (Http://www.helderbergnaturereserve.co.za), as well as patches of Renosterveld vegetation (Van Wyk & Smith 2001). At 385 hectares, HNR is the smallest of the three protected areas in this study, and information on climate and soil of this protected area is limited. However, the climate is likely to be very similar to Jonkershoek Nature Reserve. To date, no studies have been conducted on the Argentine ant at this protected area, although this species was recorded in the reserve for the first time by Boonzaaier (2006) in 2004.

Jonkershoek Nature Reserve (34°58' S, 18°56'E) is situated approximately 15 km south-east of Stellenbosch, and covers an area of 9 800 hectares. In addition to the Fynbos vegetation (Van Wyk & Smith 2001) inside the reserve, there is a large pine plantation neighboring, although not officially part of this protected area. The mean annual rainfall of the area is approximately 1600 mm, and temperatures fluctuate between approximately 1°C and 39°C, with a mean monthly maximum temperature of approximately 23°C in January and a mean monthly minimum of approximately 8°C in July (De Kock 1990). Since its introduction into this protected area (it was first recorded in 1979 by Donnelly and Giliomee (1985), the impacts of the Argentine ant on seed dispersal (Witt 1993; Witt & Giliomee 2004) and on the diversity of local ant fauna (De Kock 1990) have been studied.

Kogelberg Biosphere Reserve (34°19' S, 18°58'E) is situated approximately 90 km south-east of Cape Town and covers a total area of 20 000 ha. The reserve has an average annual rainfall of 1000-1500 mm (Van Wilgen & Richardson 1985; Johns & Johns 2001), and temperatures vary between 2 °C and 35 °C (Boucher 1978). The vegetation includes undisturbed Fynbos communities, and also areas of old cultivation and pine and eucalypt windbelts (Bond & Slingsby 1984). The impact of the Argentine ant on germination rates, as well as on seed dispersal at this protected area were studied by Bond and Slingsby (1984) and Christian (2001).

Sampling

Sampling was done between February and April 2005, October and November 2005 and January and February 2006 (encompassing peak activity periods for ants, including the Argentine Ant) (Schlettwein & Giliomee 1987; Johnson 1992). Each reserve was divided into grid cells of the same size using 1: 50 000 topographic maps (obtained from Surveys and Mapping, Mowbray, Cape Town, South Africa). Grid cells were created in Arcview version 3.2 with latitude and longitude intervals of 25 seconds (i.e. quarter-degree/minute grid cells at ca 0.17 km^2). However, Kogelberg Biosphere Reserve, which is the largest of the three reserves, was, for logistic reasons, sampled using two different grid sizes. First, a larger grid with one minute intervals (ca. 2.8 km^2) was used to cover the entire nature reserve, and thereafter smaller (25 seconds interval) grid cells were used. All accessible cells of the largest grid size were surveyed for the Argentine ant. For each grid cell, five bait stations were placed as close to the center of the grid as possible. In cases where the center of the grid was inaccessible (due to physical constraints such as thick vegetation or a mountainous area), bait stations were placed at the most accessible point closest to the center of the grid cell. To ensure that each sample was independent of the other, a minimum distance of 10 m between bait stations was maintained (Human & Gordon 1996; Andersen *et al*. 2002; Parr *et al*. 2004; Netshilaphala *et al*. 2005; Botes *et al*. 2006). In addition to the five bait stations placed in each grid cell, additional bait stations were placed at different microhabitats inside each nature reserve. Four microhabitats were sampled at Jonkershoek Nature Reserve, and five at Helderberg and Kogelberg Biosphere Reserves (see Table 1 for number of bait stations placed at each microhabitat). These bait stations were also always placed a minimum of 10 m apart.

Bait station trapping

Canned tuna fish in oil (approximately one teaspoon) that was used as bait (see Chapter 2 on bait station trapping and pilot study results) was placed on white, 90 mm diameter round filter paper to aid collection of the bait after 1 h exposure. This baiting method is commonly used when estimating the species richness and composition of epigaeic ant fauna, as well as to examine the activities and behavior of ants (Bestelmeyer *et al*. 2000). This method is also a very useful tool for comparing ant species in terms of different components of competitive ability and can provide information on habitat use (Hölldobler & Wilson 1990; Bestelmeyer 1997)). However, this method does have some disadvantages. It is difficult to standardize when using it to compare invertebrate abundances between sites (Sutherland 1996). Also, not all ant species are attracted to the type of bait used and several species will not be sampled with this method (Sutherland 1996). Although the species attracted to the bait are most likely to be generalists, these generalists do represent a large proportion of ant faunas around the world and may be used to examine some patterns in ant communities (Bestelmeyer *et al*. 2000). They are also likely to include the native ant species that would compete most directly with the Argentine ant for food resources (Sanders *et al*. 2003). Argentine ant workers are epigaeic (they forage above ground) and they interact with many epigaeic native ant species, often leading to the exclusion of native ants (Human & Gordon 1996). Several similar studies conducted elsewhere in the world have used this baiting method to assess the interaction and competition between the Argentine ant and native epigaeic ant fauna (Ward 1987; Human & Gordon 1996, 1999; Holway 1998a, 1999; Thomas & Holway 2005). In this study, bait stations were thus used to quantify the distributional range of the Argentine ant inside three protected areas in the Western Cape Province, South Africa.

Baits were covered with wire mesh cages (30 x 15 cm diameter in size, with 5 mm diameter openings in mesh) to exclude larger scavengers (such as rodents, lizard and birds) from the bait. These cages had 2 cm long wires extended at the bottom for stabilizing them in the ground. At each bait station, a red and white plastic marker was tied around nearby vegetation to facilitate relocation of the bait. After one hour, all the ants feeding at the bait station were collected, placed in containers with 100 % ethanol and taken back to the laboratory where they were identified under a microscope. Ant species were identified, in most cases to genus level and in some cases to species level (identifications confirmed by Dr.

A. Botes, University of Stellenbosch). Voucher specimens are kept at the DST-NRF Center for Invasion Biology, University of Stellenbosch, South Africa.

Data analyses

Area of occupancy (AOO)

Area of occupancy is the area across which a species is found (Gaston 2003). In this study, the area occupied by the Argentine ant at each protected area (or its distribution range within the reserve), was estimated by dividing the protected area into geographic units (grid cells), and calculating the area of occupancy based on the number of grid cells (quarter-degree/minute grid cells) occupied by the Argentine ant. This method (the grid-based or number of areas occupied method), together with two other measures of species' geographic ranges, i.e. the 'linear extent' and 'area within the limits' methods, were proposed by Gaston (1994). Several previous studies have used this geographic grid-based approach (e.g. Lawton and Schroder 1977; Claridge and Wilson 1981, 1982; Godfray 1984; Leather 1985) and it has become a common approach in determining the area of occupancy of a species. The geographic grid-based measure of distribution range size is preferred over other methods such as the 'linear extent' and 'area within the limits' methods because it highlights the dependency of measured range size of a species on the scale at which it was mapped (Gaston 1994). The area of occupancy of a species declines with the decrease in scale, i.e. the finer the resolution the larger the area from which the species is found to be absent (Gaston 2003).

In this study, the entire area of a grid cell was not surveyed, and thus this method (geographic grid-based method) is likely to provide an over-estimate of the area occupied. Thus, an alternative approach was used to obtain a more conservative method of estimating the total area occupied by the Argentine ant inside protected areas. To do this, occupancy frequency distributions (*sensu* McGeoch & Gaston 2002) were compiled for each protected area to determine the number and distribution of bait stations occupied in each set (a set consists of five bait stations in a grid cell) at each protected area (see Fig. 1). Thereafter, results from the occupancy frequency distributions were used to calculate the total area occupied by the Argentine ant at each protected area using the formula given below:

= (*a* x Area of grid cell)* 0/5 + (*b* x Area of grid cell) * 1/5 + ….+ (*f* x Area of grid cell) * 5/5,

……Equation 1

Where *a* – *f* is the relative occupancy of the species in a particular occupancy class (see Fig. 1).

The total area sampled and area occupied by the Argentine ant was expressed in hectares (ha). This approach thus provides an occupancy distribution-corrected estimate of total area occupied (referred to as 'corrected area of occupancy' hereafter), and provides a more conservative estimate of area of occupancy than the grid-based method (which gives an estimate on the extent of occurrence).

The distribution range (occupied grid cells) of the Argentine ant inside each protected area was displayed on individual maps, produced using ArcGIS version 8. Geographic Information Systems (GIS) data was obtained from Surveys and Mapping, Mowbray (Cape Town, South Africa), and additional data were also obtained from the Western Cape Nature Conservation Board, Scientific Services. The geographic position of each bait station was plotted as well as the occupied status of the bait station (presence or absence of the Argentine ant).

The nonparametric Spearman's Rank Correlation Coefficient was used to identify the sign (positive or negative) and to test the significance of the relationship between Argentine ant abundance and altitude, as well as between Argentine ant occupancy and altitude. Analyses were performed in STATISTICA for windows, version 7.

Scale-area curves

Elsewhere in the world, scale-area curves have been used to determine changes in species distribution patterns over time (decline or increase) (Fagan *et al*. 2002; Wilson *et al*. 2004); to estimate the total area occupied by a species (Kunin 1998); and to predict the abundance of a species from its occupancy (He & Gaston 2000). In this study, this approach was used to compare the distribution of the Argentine ant at the three reserves, and to compare the slopes of the three relations (one for each reserve) to predict the likely rate of spread between the reserves.

Three scales were used to construct scale-area curves for each protected area. (1) The individual bait station scale: for this scale, a round 90 mm diameter (converted to km^2) filter paper disc on which the tuna bait was placed was used as the scale size (Kunin 1998; Wilson *et al*. 2004). The diameter of the disc was used as the grid size for this scale (log_{10}). Only bait stations occupied by the Argentine ant were used to determine the area of occupancy. (2) The grid cell scale: all the individual grid cells occupied by the Argentine ant were used. Because grid cells were not square, the total area of the grid cell was square-root transformed to obtain the length of one side of a grid cell. The total area of one grid cell was 0.17 km^2, resulting in

the length of one side of the grid cell as 0.41 km^2. (3) The final scale was the protected area scale, in which the total area of the nature reserve was used. The area of occupancy for all three nature reserves was plotted on one scale-area curve to aid comparison of the distribution pattern across reserves.

To produce scale-area curves (sometimes called the range-area relationships), the area of occupancy (in km^2) at each scale was plotted against scale (in km^2), and both axes were log transformed (Hartley & Kunin 2003; Wilson *et al*. 2004). The slope of the curve is indicated by the fractal dimension (D_{ij}), which gives a measure of the aggregation of the species' distribution over a range of scales (Kunin 1998; Hartley & Kunin 2003; Wilson *et al*. 2004). A maximum value of $D_{ij} = 2$ indicates aggregated distributions, while a minimum value of $D_{ij} = 0$ indicates sparse (or patchy) distributions (Wilson *et al*. 2004). Thus,

$$D_{ij} = (1-S) \times 2, \qquad \text{…Equation 2}$$

Where S is the slope of the curve.

Microhabitat preferences

Generalized Linear Models (GLZ), assuming a Poisson error distribution (log link function, Type 3 model, Dobson 2002) were used to determine the difference in mean Argentine ant abundance at different microhabitats and at each protected area. Even though ant abundance data are biased by the fact that the species are social, and by the relative position of the bait to the closest nests, abundances do provide comparative estimates within a single species across different microhabitats. For large sample sizes, abundance does provide a proxy for the species' microhabitat preference (Ward 1987). Nonetheless, presence and absence data (occupancy) were also used. Abundance and occupancy were thus compared between microhabitats inside each protected area, and also between the three protected areas (HNR, JNR and KBR). To test for significant differences in the Argentine ant occupancy (presence and absence) between protected areas and between microhabitats at each protected area, chi-square analysis was used (Zar 1984). Helderberg Nature Reserve and Kogelberg Biosphere Reserve had all five microhabitats (building, lawn, road, vegetation and adjacent to waterbodies), whereas Jonkershoek Nature Reserve had four of the five (no lawn is present in this reserve). However, because the sample size for buildings at JNR was very low (three samples collected), this microhabitat was also excluded from all analysis. Thus, only three microhabitats (road, vegetation and adjacent to waterbodies) were considered for analysis at

JNR. Because the protected areas did not all have the same microhabitats, each reserve was analyzed separately.

RESULTS

Distribution and occupancy

Of the three protected areas sampled in this study, i.e. Helderberg Nature Reserve (HNR), Jonkershoek Nature Reserve (JNR) and Kogelberg Biosphere Reserve (KBR), HNR had the highest Argentine ant occupancy, with 71.5 % of the total bait stations occupied by the Argentine ant (Table 1). Jonkershoek Nature Reserve and KBR both had less than 50 % of the total bait stations occupied by the Argentine ant (Table 1). The edge between invaded and uninvaded areas could be clearly identified at all three protected areas in this study (see Appendix 1 for display of records without baseline layers, including the edges). *Pheidole capensis*, a dominant native ant species, was found occupying those uninvaded bait stations at the edge at JNR and KBR (Appendix 1), while *Lepisiota* sp. 1 was more abundant than *P. capensis* at the edge at HNR.

There was a significant negative correlation (at $p < 0.05$) between altitude and Argentine ant abundance at HNR (-0.380), at JNR (-0.239) and at KBR (-0.275). Similarly, there was also a significant negative correlation (at $p < 0.05$) between altitude and Argentine ant occupancy at all three protected areas (HNR = -0.359, JNR = -0.256 and KBR = -0.320). Thus, the abundance and occupancy of the Argentine ant at all three protected areas in this study decreased with the increase in altitude, although the altitudinal limits at each reserve were very different (Fig. 2).

At HNR, the Argentine ant was distributed across most of the protected area, particularly across the lower altitudinal areas (Fig. 2A) The highest altitude from where the Argentine ant was recorded at HNR was 342 m (Fig. 2A), while the highest altitude sampled was 439 m (the Argentine ant was absent at this altitude). A total area of 272 ha, divided into five grid cells and covering most of the reserve (excluding the mountainous area), was sampled at HNR. Four of the five sampled grid cells were occupied by the Argentine ant (Fig. 3A), resulting in a total estimated area occupied by the Argentine ant of 220 ha (80 % of the reserve area) (Table 2, grid-based method). Based on the 'corrected area of occupancy' method (see Equation 1), the total area occupied by the Argentine ant at HNR was much reduced at 48 ha (Table 2). Inside this protected area, the Argentine ant was found at higher abundances and occupancies in areas around the buildings and at picnic spots (lawn area) than adjacent to

waterbodies (streams and ponds), along roadsides and in natural vegetation (Fig. 4a. A, Fig. 4b.A).

A total area of 920 ha (divided into 25 grid cells) was sampled for the prevalence of the Argentine ant inside JNR, and 440 ha (16 grid cells; 48 % of reserve area) were occupied by the Argentine ant. Results of the 'corrected area of occupancy' method estimated that the area occupied by the Argentine ant is 204 ha, again lower than the grid-based method (Table 2). The highest altitude from which the Argentine ant was recorded at JNR was 511 m (at the fire 'look-out' station), while 571 m was the highest altitude sampled (Fig. 2B). The second highest occupied altitude was 446 m (Fig 2B). The distribution range of the Argentine ant inside JNR stretched from the reserve entrance until a few meters past the Swartboskloof Valley (Fig. 3B). Most of the eastern side of JNR, including the Witbrug picnic area, remains uninvaded by the Argentine ant (Fig. 3B). The Argentine ant was most abundant inside the vegetation (Fynbos and pine plantation), followed by along waterbodies, than it was along the gravel road (the circular route) that runs through the reserve (Fig. 4b. B).

Kogelberg Biosphere Reserve was the largest protected area sampled in this study, with a total area of 5800 ha sampled, and only 50 ha occupied by the Argentine ant (0.9 % of reserve area). However, based on the 'corrected area of occupancy' method, only 31 ha were occupied by the Argentine ant at KBR. All the occupied bait stations at KBR were at an altitude below 100 m, with the highest occupied bait station at 95 m (Fig. 2C). The highest sampled altitude was at 546 m. Argentine ants were only found in one grid cell at KBR, and this grid cell includes all the buildings in the protected area, i.e. reserve offices, over-night visitors accommodation and the reserve manager's house (Fig. 3C). *Pheidole capensis* occupied more grid cells than the Argentine ant, and was also found in the same grid cell with the Argentine ant, although not occupying the same bait stations (Appendix 1).

Generally, the Argentine ant was sparsely distributed at all three protected areas, as revealed by the fractal dimensions and slopes of the scale-area curves compared with the slope of the minimum area of occupancy (Table 3; Fig. 5). Kogelberg Biosphere Reserve was the most sparsely distributed, followed by JNR and then HNR (Table 3). There were significant differences in the Argentine ant abundance (d.f. = 849, deviance = 81750.20, scaled deviance / d.f. = 96.29; d.f. = 2, X^2 = 133.31, $p < 0.001$) and occupancy (d.f. = 2, X^2 = 59.59, $p < 0.001$) among protected areas. On average, HNR had the highest Argentine ant abundance per bait station, followed by JNR, while KBR had the lowest abundance per bait station (Fig. 6).

Microhabitat preferences

There were significant differences in the Argentine ant abundance between microhabitats at HNR (d.f. = 153, deviance = 14752.86, scaled deviance / d.f. = 96.42; d.f. = 4, X^2 = 66.72, p < 0.001), at JNR (d.f. = 420, deviance = 50188.8, scaled deviance / d.f. = 119.46; d.f. = 2, X^2 = 33.46, p < 0.001), and at KBR (d.f. = 263, deviance = 3794.4, scaled deviance / d.f. = 14.42; d.f. = 4, X^2 = 160.74, p < 0.001). Similarly, there were significant differences in the Argentine ant occupancy between microhabitats at HNR (d.f. = 4, X^2 = 30.81, p < 0.001), JNR (d.f. = 2, X^2 = 22.34, p < 0.001), and KBR (d.f. = 4, X^2 = 81.41, p < 0.001). Buildings and lawn microhabitats had the highest abundances (Fig. 4a) and occupancies (Fig. 4b) at all three protected areas. At HNR, occupancy adjacent to waterbodies, i.e. rivers, streams and ponds, was also high, but not at JNR and KBR (Fig. 4b). Thus, the Argentine ant was only found along waterbodies in areas where it was also more generally abundant (see Fig. 3). Other microhabitats, i.e. along roadside and in natural vegetation, sampled at each nature reserve were also occupied, although at lower percentage occupancies than at buildings and lawn (Fig. 4b).

DISCUSSION

Although studies have previously been conducted on the Argentine ant at two of the three protected areas in this study (JNR and KBR) (*sensu* Bond & Slingsby 1984; De Kock 1990; Witt 1993; Witt *et al*. 2004; Christian 2001), this is the first study quantifying the distribution range of the Argentine ant inside these protected areas. All the studies conducted before the current one investigated the impact of the Argentine ant on seed dispersal and seedling emergence, and few have made observations regarding the impact of this species on native ant species richness. Thus, till this study, the extent of invasion by the Argentine ant inside the three protected areas remained unknown.

This study shows that the Argentine ant is well established inside each of the three protected areas, however the extent of invasion varies among the reserves. The three protected areas in this study had factors that have previously been shown to be conducive to the invasion and spread of the Argentine ant, e.g. highly disturbed areas such as buildings, picnic sites with rubbish bins, permanent water sources and roads (Ward 1987; De Kock 1990; Menke & Holway 2006). In this study, the Argentine ant showed a clear preference for human influenced areas, particularly close to buildings and at picnic sites (on lawns). This finding is

consistent with findings of other studies, which also showed that the Argentine ant has a preference for highly disturbed areas, particularly close to human dwellings (De Kock 1990; Holway 1998b; Carpintero *et al*. 2003). In California, moisture availability has been shown to facilitate the spread of the Argentine ant (Ward 1987; Human *et al*. 1998). However, results of the three reserves presented here showed that the Argentine ant only occurred adjacent to waterbodies in areas where it was also more generally abundant. Therefore, although moisture availability may play a role in influencing the establishment of the Argentine ant inside these protected areas, there was no evidence that waterbodies per se, i.e. rivers and streams, facilitates its spread inside these protected areas. This result contradicts that of Witt *et al*. (2004), who suggested that the presence of the Argentine ant inside JNR is associated with the availability of water, i.e. streams. The three protected areas in this study are all in close proximity to human settlements, and thus these urban areas are potential sources of the Argentine ant invasion. However, HNR is much closer to an urban settlement, i.e. within walking distance, than JNR and KBR (see Fig. 3). New populations of the Argentine ant may spread into these adjacent protected areas both naturally and through unintentional transportation by humans (Carpintero *et al*. 2003).

Argentine ants were more abundant and widely distributed at lower altitudinal areas at all three protected areas, and the highest altitude at which they were found was 511 m (at JNR). The latter record was isolated and made at the fire 'look-out' station (a small building used to monitor fire in the plantation), which is regularly occupied by a person on fire-watch. The nearest Argentine ant record to the 'look-out' station was *ca*. 250 m away from the closest presence record. Thus, Argentine ants were probably introduced to this station via human-mediation and have not spread via nest budding to this point. Human *et al*. (1998) also found that populations of the Argentine ant were well established in areas with lower altitudes in northern California. However, other studies have shown that the Argentine ant' distribution range is not limited by the increase in altitude, as populations of this species have been recorded from altitudes higher than 1000 m, e.g. in Hawaii (Krushelnycky *et al*. 2005). In a previous study, Way *et al*. (1997) found that although the Argentine ant occurred mainly at lower altitudinal areas, it was also common on mountainous tops, and that there was no relationship between the Argentine ant's distribution and height above the valley floor. Argentine ants were more common at lower altitudes at each reserve, where most human-modified habitats are situated, although the protected areas in this study had different altitude limits. This suggests that the spread and establishment of the Argentine ant is not limited by altitude, but rather by its association with anthropogenic disturbances. Thus, when spreading naturally through budding of the nest after introduction, Argentine ants will occupy lower

altitudinal areas rather than higher areas purely because this is where most human-mediated introductions occur and where the highest levels and largest areas of human disturbances occur. Nonetheless, Argentine ant populations will also readily establish their populations at high altitude areas if introduced there by humans.

Helderberg Nature Reserve, which is the smallest of the three protected areas and is completely surrounded by urban and agricultural areas, had the largest surface area and the most number of bait stations occupied by the Argentine ant. Since most parts of HNR are accessible on foot, the distribution of the Argentine ant inside this reserve could be a combined effect of natural nest diffusion and human-mediation, and this may result in a high rate of spread for the Argentine ant.

This study also showed that at JNR the Argentine ant has spread a maximum of approximately 160 m from Swartboskloof Valley eastward, since the previous survey conducted by De Kock (1990) and Witt (1993) in this valley. This distance was obtained by comparing the distribution map of the Argentine ant in Swartboskloof Valley by De Kock *et al*. (1992) with the distribution map in the current study. Thus, the rate of spread of the Argentine ant inside JNR has been relatively slow over the years. Studies conducted in California have shown that the natural rate of spread for the Argentine ant is very slow (*ca*. 100 m/year) (Erickson 1971; Holway 1995). The Argentine ant was abundant along the gravel circular road inside JNR in the current study, and this road could potentially facilitate the spread of this species within the reserve. De Kock and Giliomee (1989) demonstrated that the probability of the Argentine ant infestation in various Fynbos areas across the Western Cape Province increases with ease of access, i.e. areas with vehicle access by gravel or tarred road have a higher probability of the Argentine ant infestation. However, it was surprising that the 'Witbrug' area in this reserve, which is one of the most frequently visited areas, with high human traffic on a daily basis, particularly during summer months was free of Argentine ants. It is therefore unclear why the Argentine ant has not been able to spread into this area. In addition, this area includes some of the factors that are conducive to invasion (a perennial river, rubbish bins and parking area for cars). It is possible that this species is experiencing biotic resistance from native ant species such as *Pheidole capensis* (a myrmecochorus ant species), which was found to be the most dominant native ant species in this area. In Australia, Walters and Mackay (2005) demonstrated that dominant native ant species may resist invasion and limit the spread of the Argentine ant, particularly if the native ant is numerically dominant than the Argentine ant. However, several studies have demonstrated that the Argentine ant displaces *P. capensis* in invaded areas at JNR (Donnelly & Giliomee 1985; De Kock 1990; Witt *et al*. 2004). Thus, in time, the Argentine ant could spread to this

uninvaded area and displace more native ant species, including *P. capensis*. It is suspected that the Argentine ant was introduced into JNR with pine seedlings for forestry reasons (Giliomee, pers. comm.). This introduction pathway may allow for both workers and queens to be successfully transported into a new area, allowing for successful establishment of a new colony. The pine plantation in JNR is not in close proximity to the Witbrug area, which could also explain why this area remains uninvaded by the Argentine ant.

At KBR the Argentine ant was absent from most parts of the reserve and was restricted to areas around buildings. Thus, the Argentine ant has not spread long distances since the study by Bond and Slingsby (1984) conducted at this part of the reserve, known as Oudebosch (although the exact locality where Bond and Slingsby conducted their study inside KBR is not clear from their publication). *Pheidole capensis* was the most dominant species in most parts of the reserve, and could be resisting invasion by the Argentine ant. However, as in JNR, previous studies (Bond and Slingsby 1984; Christian 2001) have shown that the Argentine ant has displaced *P. capensis* from invaded areas at KBR. This is the largest of the three protected areas studied here, and access to the rest of the reserve is by foot, with limited vehicle use by reserve management. Thus, any range expansion of the Argentine ant inside KBR that may be occurring is primarily through nest budding, and there is no evidence of large distance human-mediated range expansion by the Argentine ant in the reserve since 1984.

Uninvaded bait stations at the invasion front (the edge between invaded and uninvaded areas) were dominated by the common seed disperser ant, *Pheidole capensis*, particularly at JNR and KBR (see Appendix 1 for the edges). This species (*P. capensis*) and other native ant species occurring at the edge are potentially vulnerable to an edge effect caused by the Argentine ant, particularly during peak activity season for the Argentine ant. In southwestern California, Holway (2005) demonstrated that the Argentine ant suppressed both the abundances and species richness of native ants occurring at invasion edges. At KBR, *Tetramorium quadrispinosum* was also found at bait stations occurring at the invasion edge, while *Lepisiota* sp. 1 was more abundant than *P. capensis* at the edge at HNR.

The findings of this study and other previous studies (*sensu* Holway 1998b; DiGirolamo & Fox 2006) strongly suggest that the establishment and spread of the Argentine ant in its introduced ranges (post introduction) is largely enhanced by abiotic factors, particularly anthropogenic disturbances. Altitude and the availability of free-standing water bodies does not appear to play a role in influencing the distribution of the Argentine ant inside the protected areas that were examined, although studies conducted elsewhere demonstrated that soil moisture facilitates its spread (Holway 1995; Espadaler & Gómez 2003; Menke & Holway 2006). A combination of biotic factors, i.e. interspecific competition (biotic

resistance) from native ant species, and abiotic factors, i.e. lack of soil moisture, could limit the spread of the Argentine ant at the invasion front (Ward 1987; Holway 1998b; Holway 2005). The natural rate of spread of the Argentine ant inside the three protected areas was generally low, and is thus consistent with the slow rates of natural spread shown elsewhere in the world (Erickson 1971; Holway 1995). However, unrestricted human activities inside the reserves, including the use of vehicles, could nonetheless rapidly facilitate the spread and increase in extent of its invasion in these reserves (De Kock 1990). Argentine ants were clearly shown to be associated with human-modified landscapes and could thus readily be transported to uninvaded parts of the reserve by human activity. Thus, to limit the spread of the Argentine ant inside protected areas, human activities inside reserves should be limited. In particular, activities such as the movement of soil, e.g. in pot plants and for building constructions, which may transport an entire Argentine ant nest (workers and queens) to other parts of the reserve, should be limited. It is therefore recommended that any future recreational development, particularly buildings, should be limited to one point of the reserve, preferably closer to the edge of the protected area.

REFERENCES

ADDISON, P. & SAMWAYS, M.J. 2000. A survey of ants (Hymenoptera: Formicidae) that forage in vineyards in the Western Cape Province, South Africa. *African Entomology* **8**: 251-260.

ADDISON, P. & SAMWAYS, M.J. 2006. Surrogate habitats demonstrate the invasion potential of the African pugnacious ant. *Biodiversity and Conservation* **15**: 411-428.

ANDERSEN, A.N., HOFFMANN, B.D., MÜLLER, W.J. & GRIFFITHS, A.D. 2002. Using ants as bioindicators in land management: simplifying assessment of ant community responses. *Journal of Applied Ecology* **39**: 8-17.

BESTELMEYER, B.T. 1997. Stress tolerance in some Chacoan dolichoderine ants: implications for community organization and distribution. *Journal of Arid Environments* **35**: 297-310.

BESTELMEYER, B.T., AGOSTI, D., ALONSO, L.E., ROBERTO, C., BRANDAO, F., BROWN, W.L. (Jr)., DELABIE, J.H.C., & SILVESTRE, R. 2000. Field techniques for the study of ground-dwelling ants. In: Agosti, D., Majer, J.D., Alonso, L.E. & Schultz, T.R. (Eds). *Ants*: *standard methods for measuring and monitoring biodiversity*. 122-144. Smithsonian Institution Press, Washington, London.

BOND, W.J. & SLINGSBY, P. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorus Proteaceae. *Ecology* **65**: 1031-1037.

BOONZAAIER, C. 2006. *Conservation in human-influenced areas*: *epigaeic arthropods in the Cape Floristic Region lowlands*. MSc Thesis, University of Stellenboch, Stellenbosch.

BOTES, A., MCGEOCH, M.A., ROBERTSON, H.G., VAN NIEKERK, A., DAVIDS, H.P. & CHOWN, S.L. 2006. Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* **33**: 71-90.

BOUCHER, C. 1978. Cape Hangklip area. II. The vegetation. *Bothalia* **12**: 455-497.

CARPINTERO, S., REYES-LÓPEZ, J., & ARIAS DE REYNA, L. 2003. Impact of human dwellings on the distribution of the exotic Argentine ant: a case study in the Doñana National Park, Spain. *Biological Conservation* **115**: 279-289.

CHRISTIAN, C.E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* **413**: 635-639.

CLARIDGE, M.F. & WILSON, M.R. 1981. Host plant associations, diversity and species-area relationships of mesophyll-feeding leafhoppers of trees and shrubs in Britain. *Ecological Entomology* **6**: 217-238.

CLARIDGE, M.F. & WILSON, M.R. 1982. Insect herbivore guilds and species-area relationships of leafminers on British trees. *Ecological Entomology* **7**: 19-30.

COWLING, R.M. & HOLMES, P.M. 1992. Flora and vegetation. In: Cowling, R. (Ed.) *The Ecology of Fynbos: Nutrients, Fire and Diversity*. 23-61. Oxford University Press, Cape Town.

CRAWLEY, M.J., BROWN, S.L., HEARD, M.S. & EDWARDS, G.R. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* **2**: 140-148.

DE KOCK, A.E. 1990. *The Argentine ant,* Iridomyrmex humilis *Mayr, indigenous ants and other epigaeic invertebrates of the fynbos in relation to fire and vegetation age*. MSc Thesis, University of Stellenboch, Stellenbosch.

DE KOCK, A.E. & GILIOMEE, J.H. 1989. A survey of the Argentine ant, *Iridomyrmex humilis* (Mayr) (Hymenoptera: Formicidae) in South African Fynbos. *Journal of the Entomological Society of Southern Africa* **52**: 157-164.

DE KOCK, A.E., GILIOMEE, J.H., PRINGLE, K.L. & MAJER, J.D. 1992. The influence of fire, vegetation age and Argentine ants (*Iridomyrmex humilis*) on ant communities in Swartboskloof. In: Van Wilgen, B.W., Richardson, D.M., Kruger, F.J. & Van Hensbergen, H.J. (Eds). *Fire in South African Mountain Fynbos*. 203-215. Springer-Verlag, Berlin.

DIGIROLAMO, L.A. & FOX, L.R. 2006. The influence of abiotic factors and temporal variation on local invasion patterns of the Argentine ant (*Linepithema humile*). *Biological Invasions* **8**: 125-135.

DOBSON, A.J. 2002. An introduction to generalized linear models. Chapman and Hall.

DONNELLY, D. & GILIOMEE, J.H. 1985. Community structure of epigaeic ants (Hymenoptera: Formicidae) in Fynbos vegetation in the Jonkershoek valley. *Journal of the Entomological Society of Southern Africa* **48**: 247-257.

ELTON, C.S. 1958. The ecology of invasions by animals and plants. Methuen, London.

ERICKSON, J.M. 1791. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. *Psyche* **78**: 257-266.

FAGAN, W.F., UNMACK, P.J., BURGESS, C. & MINCKLEY, W.L. 2002. Rarity, fragmentation, and extinction risk in desert fishes. *Ecology* **83**: 3250-3256.

FLUKER, S.S. & BEARDSLEY, J.W. 1970. Sympatric associations of three ants: *Iridomyrmex humilis*, *Pheidole megacephala*, and *Anoplolepis longipes* in Hawaii. *Annals of the Entomological Society of America* **63**: 1290-1296.

GASTON, K.J. 1994. Measuring geographic range sizes. *Ecography* **17**: 198-205.

GASTON, K.J. 2003. *The structure and dynamics of geographic ranges*. Oxford University Press, New York.

GODFRAY, H.C.J. 1984. Patterns in the distribution and of leafminers on British trees. *Ecological Entomology* **9**: 163-168.

HARTLEY, S. & KUNIN, W.E. 2003. Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology* **17**: 1559-1570.

HE, F. & GASTON, K.J. 2000. Estimating species abundance from occurrence. *The American Naturalist* **156**: 553-559.

HÖLLDOBLER, B. & WILSON, E.O. 1990. *The ants*. Harvard University Press, Cambridge, Massachusetts.

HOLWAY, D.A. 1995. Distribution of the Argentine ant (*Linepithema humile*) in Northern California. *Conservation Biology* **9**: 1634-1637.

HOLWAY, D.A. 1998a. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia* **116**: 252-258.

HOLWAY, D.A. 1998b. Factors governing rate of invasion: a natural experiment using Argentine ants. *Oecologia* **115**: 206-212.

HOLWAY, D.A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* **80**: 238-251.

HOLWAY, D.A. 2005. Edge effects of an invasive species across a natural ecological boundary. *Biological Conservation* **121**: 561-567.

HOLWAY, D.A., SUAREZ, A.V. & CASE, T.J. 2002. Role of abiotic factors in governing susceptibility to invasion: A test with Argentine ants. *Ecology* **83**: 1610-1619.

HUMAN, K.G. & GORDON, D.M. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* **105**: 405-412.

HUMAN, K.G. & GORDON, D.M. 1999. Behavioral interactions of the invasive Argentine ant with native ant species. *Insectes Sociaux* **46**: 159-163.

HUMAN, K.G., WEISS, S., WEISS, A., SANDLER, B. & GORDON, D.M. 1998. Effects of abiotic factors on the distribution and activity of the invasive Argentine ant (Hymenoptera: Formicidae). *Environmental Entomology* **27**: 822-833.

JENKINS, P.T. 1996. Free trade and exotic species introductions. *Conservation Biology* **10**: 300-302.

JOHNS, A. & JOHNS, M. 2001. *Kogelberg Biosphere Reserve*: heart of the Cape flora. Struik Publishers.

JOHNSON, S.D. 1992. Plant-animal relationships. In: Cowling, R.M. (Ed). *The ecology of fynbos: Nutrients, fire and diversity*. 175-205. Oxford University Press, Cape Town.

KEANE, R.M. & CRAWLEY, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* **17**: 164-170.

KRUSHELNYCKY, P.D., JOE, S.M., MEDEIROS, A.C., DAEHLER, C.C. & LOOPE, L.L. 2005. The role of abiotic conditions in shaping the long-term patterns of a high-elevation Argentine ant invasion. *Diversity and Distributions* **11**: 319-331.

KUNIN, W.E. 1998. Extrapolating species abundance across spatial scales. *Science* **281**: 1513-1515.

LAWTON, J.H. & SCHROEDER, D. 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature* **265**: 137-140.

LEATHER, S.R. 1985. Does the bird cherry have its fair share of insect pests? An appraisal of the species-area relationships of the phytophagous insects associated with British Prunus species. *Ecological Entomology* **10**: 43-56.

LE MAITRE, D.C., VAN WILGEN, B.W., CHAPMAN, R.A. & MCKELLY, D.H. 1996. Invasive plants and water resources in the Western Cape Province, South Africa: modeling the consequences of a lack of management. *Journal of Applied Ecology* **33**: 161-172.

LOWE, S., BROWNE, M., BOUDJELAS, S. & DE POORTER, M. 2000. 100 of the world's worst invasive alien: a selection from the Global Invasive Species Database. *The Invasive Species Specialist Group (ISSG), World Conservation Union (IUCN).*

MARKIN, G.P. 1970. The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae), in Southern California. *Annals of the Entomological Society of America* **63**: 1238-1242.

MCGEOCH, M.A. & GASTON, K.J. 2002. Occupancy frequency distributions: patterns, artifacts and mechanisms. *Biological Review* **77**: 311-331.

MCGLYNN, T.P. 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography* **25**: 535-548.

MENKE, S.B. & HOLWAY, D.A. 2006. Abiotic factors control invasion by Argentine ants at a community scale. *Journal of Animal Ecology* **75**: 368-376.

MOLL, E.J. & JARMAN, M.L. 1984. Clarification of the term fynbos. *South African Journal of Science* **80**: 351-352.

NETSHILAPHALA, N.M., MILTON, S.J. & ROBERTSON, H.G. 2005. Response of an ant assemblage to mining on the arid Namaqualand coast, South Africa. *African Entomolgogy* **13**: 162-167.

PARR, C.L., ROBERTSON, H.G., BIGGS, H.C. & CHOWN, S.L. 2004. Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology* **41**: 630-642.

PASSERA, L. 1994. Characteristics of tramp species. In: Williams, D.F. (Ed). *Exotic ants*: *biology, impact and control of introduced species*. 23-43. Westview Press, Colorado, USA.

PRINS, A.J., ROBERTSON, H.G. & PRINS, A. 1990. Pest ants in urban and agricultural areas of Southern Africa. In: Vander Meer, R.K., Jaffe, K, & Cedeno, A. (Eds). *Applied myrmecology*: *a world perspective*. 25-33. Westview Press, Colorado, USA.

REIMER, N.J. 1994. Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. In: Williams, D.F. (Ed). *Exotic ants*: *biology, impact and control of introduced species*. 11-22. Westview Press, Colorado, USA.

SANDERS, N.J., GOTELLI, N.J. HELLER, N.E. & GORDON, D.M. 2003. Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences of the United States of America* **100**: 2474-2477.

SCHLETTWEIN, C.H.G. & GILLIOMEE, J.H. 1987. Comparison of insect biomass and community structure between fynbos sites of different ages after fire with particular reference to ants, leafhoppers and grasshoppers. *Annale Universiteit van Stellenbosch* 2 (2), Serie A3 (Landbouwetenskappe).

SUAREZ, A.V., HOLWAY, D.A. & CASE, T.J. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proceedings of the National Academy of Science* **98**: 1095-1100.

SUTHERLAND, J. 1996. *Ecological census techniques – a handbook*. Cambridge University Press, UK.

THOMAS, M.L. & HOLWAY, D.A. 2005. Condition-specific competition between invasive Argentine ants and Australian *Iridomyrmex*. *Journal of Animal Ecology* **74**: 532-542.

VAN WILGEN, B.W. & RICHARDSON, D.M. 1985. The effects of alien shrub invasions on vegetation structure and fire behaviour in South African Fynbos shrublands: a simulation study. *Journal of Applied Ecology* **22**: 955-966.

VAN WYK, A.E. & SMITH, G.F. 2001. *Regions of floristic endemism in Southern Africa*: *a review with emphasis on succulents*. Umdaus Press.

VEGA, S.Y. & RUST, M.K. 2001. The Argentine ant – a significant invasive species in agricultural, urban and natural environments. *Sociobiology* **37**: 3-25.

VITOUSEK, P.M., D'ANTONIO, C.M., LOOPE, L.L., REJMÁNEK, M. & WESTBROOKS, R. 1997. Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* **27**: 1-16.

WALTERS, A.C. & MACKAY, D.A. 2005. Importance of large colony size for a successful invasion by Argentine ants (Hymenoptera: Formicidae): evidence for biotic resistance by native ants. *Austral Ecology* **30**: 395-406.

WARD, P.S. 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. *Higardia* **55**: 1-16.

WARD, D.F., BEGGS, J.R., CLOUT, A.N., HARRIS, R.J. & O'CONNOR, S. 2006. The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal. *Diversity and Distributions* **12**: 601-609.

WAY, M.J., CAMMELL, M.E., PAIVA, M.R. & COLLINGWOOD, C.A. 1997. Distribution and dynamics of the Argentine ant *Linepithema* (*Iridomyrmex*) *humile* (Mayr) in relation to vegetation, soil conditions, topography and native competitor ants in Portugal. *Insectes Sociaux* **44**: 415-433.

WILSON, R.J., THOMAS, C.D., FOX, R., ROY, D.B. & KUNIN, W.E. 2004. Spatial patterns in species distributions reveal biodiversity change. *Nature* **432**: 393-396.

WICHT, C.L., MEYBURGH, J.C. & BOUSTEAD, P.G. 1969. Rainfall at the Jonkershoek Forest Hydrological Research Station. *Annale Universiteit van Stellenbosch* 44, Serie A(1).

WITT, A.B.R. 1993. *Factors affecting myrmecochory in fynbos*. MSc Thesis, University of Stellenbosch, Stellenbosch.

WITT, A.B.R. & GILLIOMEE, J.H. 2004. The impact of an invasive ant, *Linepithema humile* (Mayr), on the dispersal of *Phylica pubescens* Aiton seeds in South Africa. *African Entomology* **12**: 179-185.

WITT, A.B.R., GEERTSEMA, H. & GILIOMEE, J.H. 2004. The impact of an invasive ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), on the dispersal of the elaiosome-bearing seeds of six plant species. *African Entomology* **12**: 223-230.

ZAR, J.H. 1984. *Biostatistical analysis*. Prentice-Hall International, Inc.

Table 1. Occupancy of the Argentine ant at bait stations in different microhabitats in three protected areas. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve and KBR = Kogelberg Biosphere Reserve. _ = this microhabitat was not present., N = total number of bait stations.

Microhabitat	**HNR**			**JNR**			**KBR**			**Total %**
	N	**No. occupied**	**% occupied**	**N**	**No. occupied**	**% occupied**	**N**	**No. occupied**	**% occupied**	
Buildings	14	14	100	3	3	100	38	37	97	98.1
Lawn	30	30	100	_	_	_	30	18	60	80
Road	54	27	50	202	52	25.7	30	22	73.3	35.3
Vegetation	31	20	64.5	166	91	54.8	155	20	12.9	37.2
Waterbodies	29	22	75.9	55	15	27.3	15	1	6.7	38.4
Total	158	113	71.5	426	161	37.8	268	98	36.6	

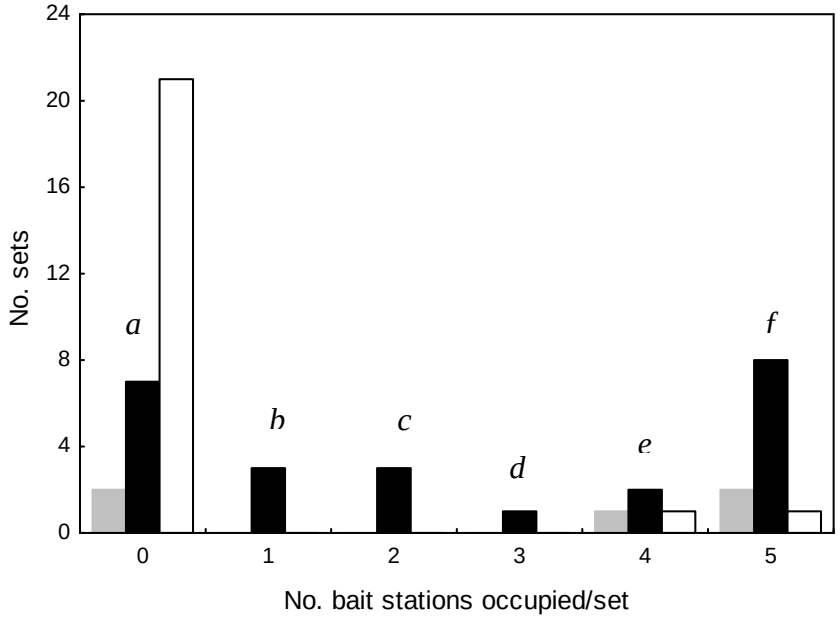
Table 2. Area (in ha) occupied by the Argentine ant at Helderberg Nature Reserve (HNR), Jonkershoek Nature Reserve (JNR) and Kogelberg Biosphere Reserve (KBR) based on two methods: Method 1 = 'Grid-based' method (gives an idea on the extent of occurrence); Method 2 = 'Corrected area of occupancy' method (gives an idea on the area of occupancy, see Equation 1).

	Area occupied (ha) (% of reserve area)		
Reserve (sampled area)	**Method 1**	**Method 2**	**Difference (ha)**
HNR (272 ha)	220 (80 %)	48 (17.6 %)	172
JNR (920 ha)	440 (48 %)	204 (22.2 %)	236
KBR (5800 ha)	50 (0.9 %)	31 (0.5 %)	19

Table 3. Fractal dimensions (D_{ij}) for the scale-area curves of three Protected Areas. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, and KBR = Kogelberg Biosphere Reserve.

Reserve	**Equation**	**R^2**	**Slope**	**D_{ij}**
HNR	$Y = 1.8526x^{0.7762}$	0.9983	0.7762	0.4476
JNR	$Y = 4.7233x^{0.7979}$	0.9935	0.7979	0.4042
KBR	$Y = 2.1355x^{0.8013}$	0.9986	0.8013	0.3974
Min AOO	Y = x	1	1	0

A.



B.

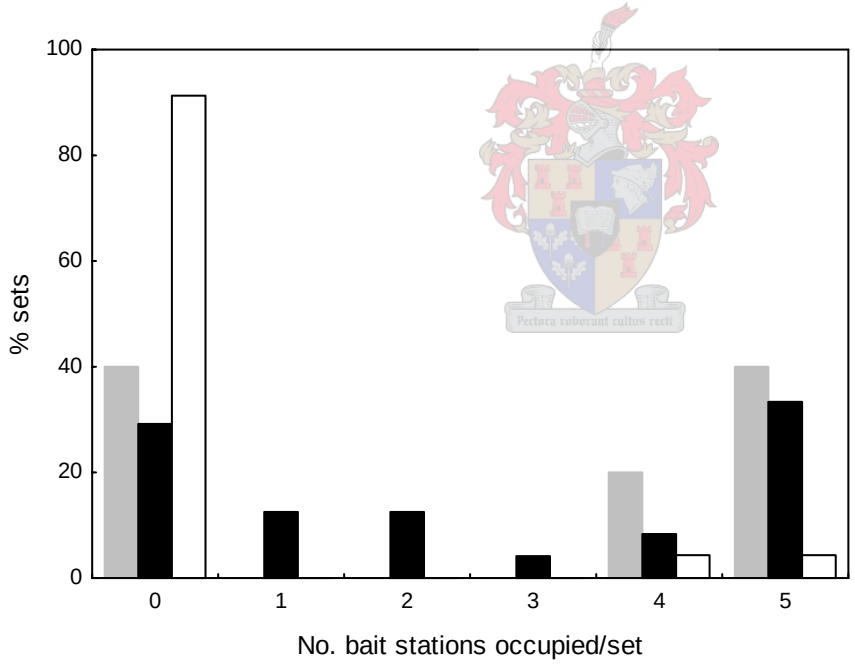


Fig. 1. Occupancy frequency distributions of **A.** number and **B.** percentage of bait stations occupied by the Argentine ant per set at Helderberg Nature Reserve (grey bars), Jonkershoek Nature Reserve (black bars) and Kogelberg Biosphere Reserve (white bars). Letters *a* – *f* were used in equation 1 to calculate the area occupied by the Argentine ant at each protected area and represent the relative occupancy of occupied bait stations in different occupancy classes.

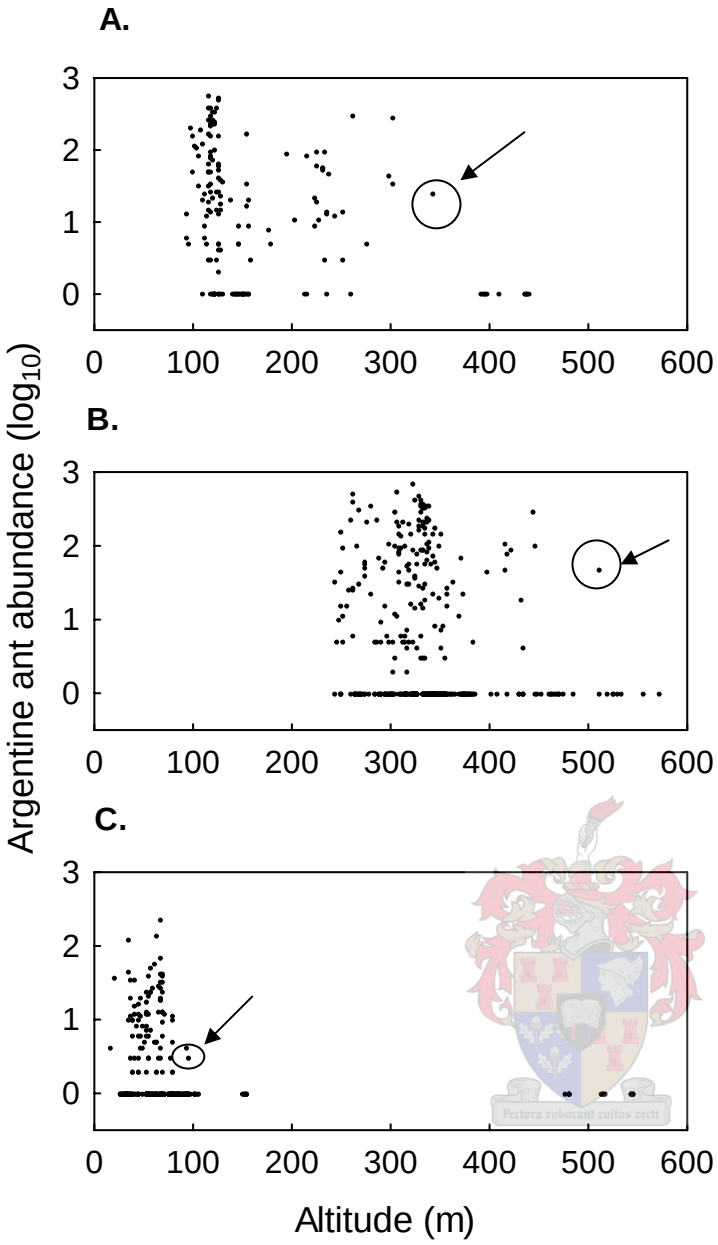


Fig. 2. Argentine ant abundances at bait stations across altitude at **A.** Helderberg Nature Reserve, **B.** Jonkershoek Nature Reserve, and **C.** Kogelberg Biosphere Reserve. Circled points indicated by an arrow = highest altitude where the Argentine ant was collected from that reserve.

A.

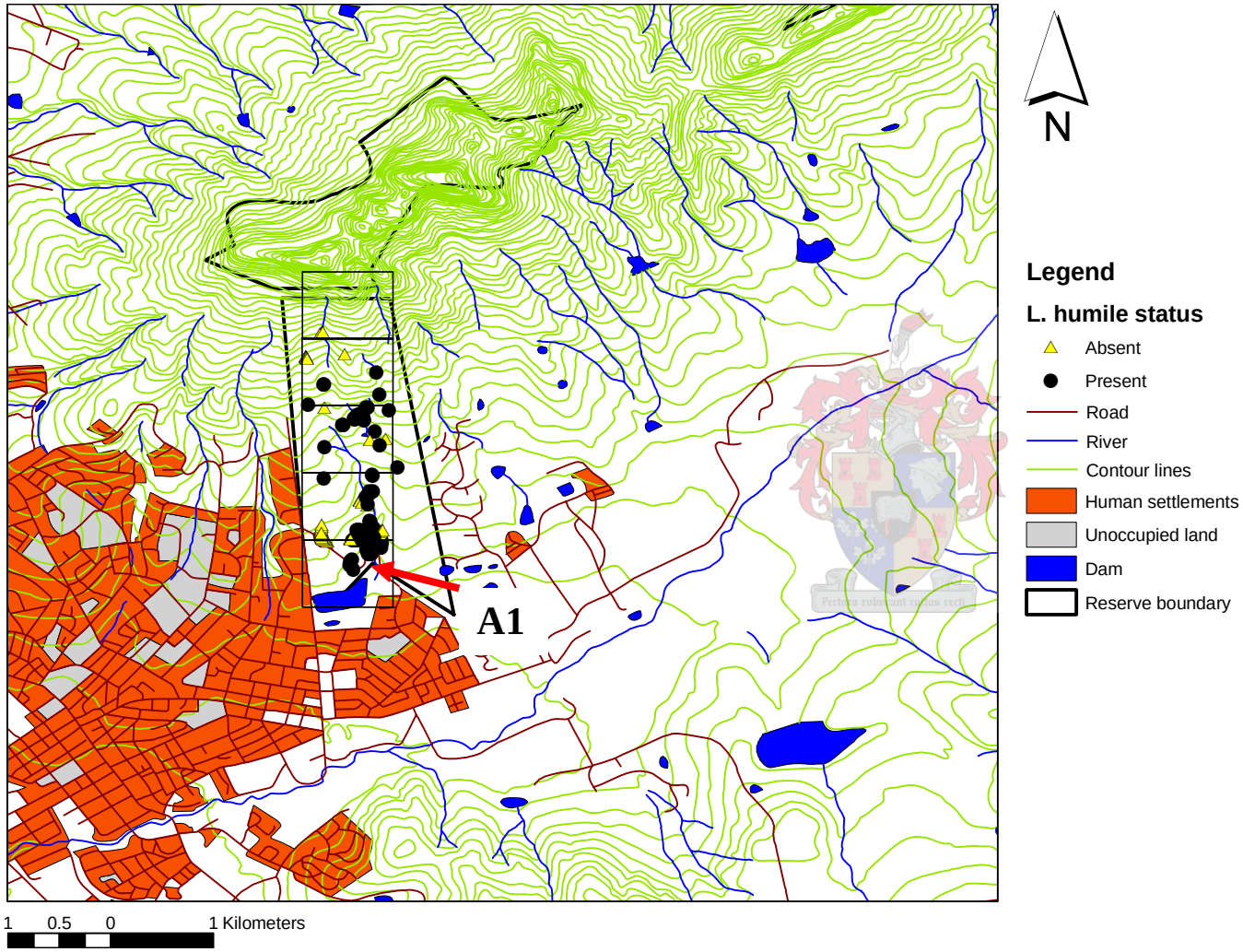

A1
N
Legend
L. humile status
Absent
Present
Road
River
Contour lines
Human settlements
Unoccupied land
Dam
Reserve boundary
1 0.5 0 1 Kilometers

Fig. 3A.

B.

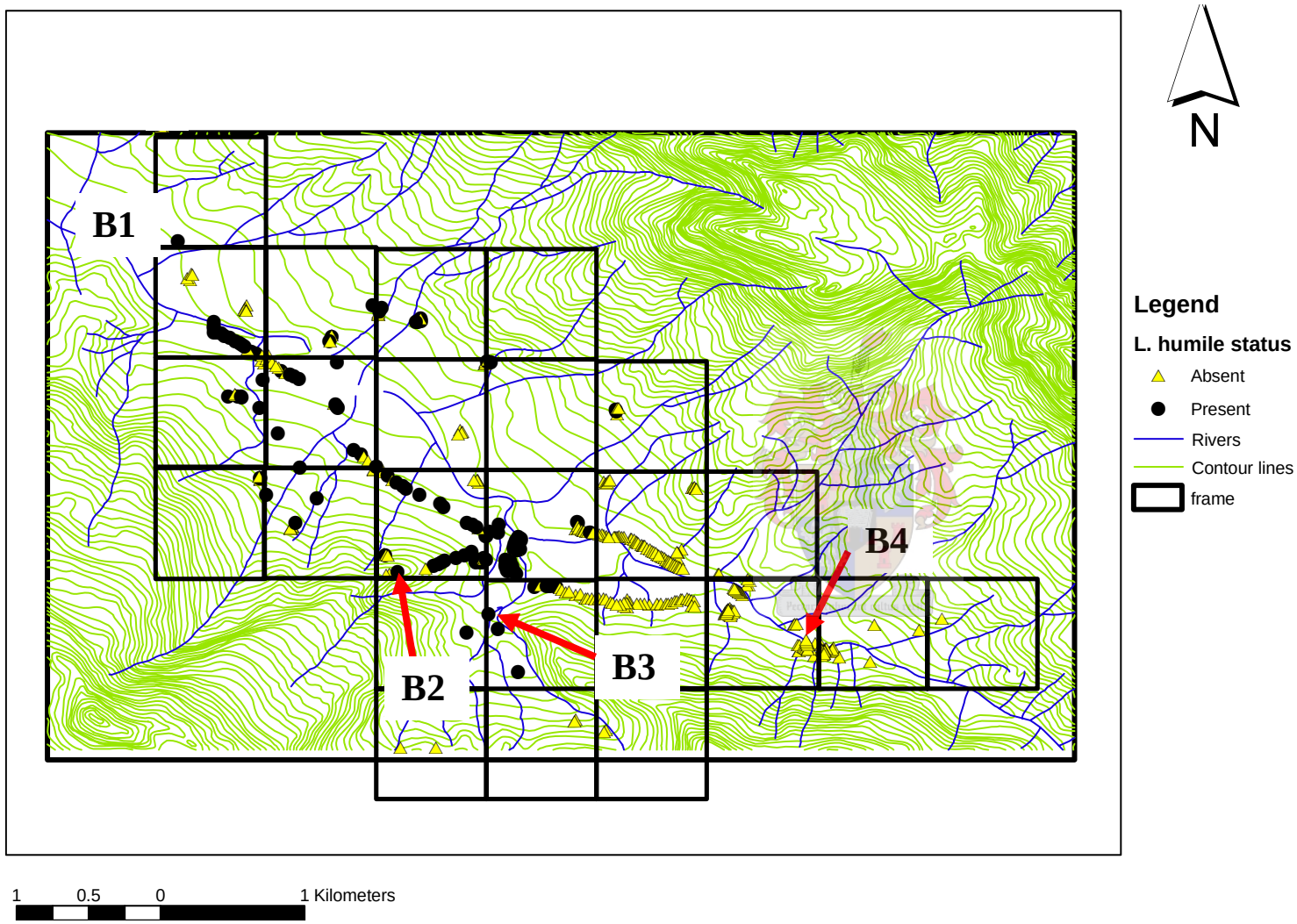

B1
B2
B3
B4
N
Legend
L. humile status
Absent
Present
Rivers
Contour lines
frame
1 0.5 0 1 Kilometers

Fig. 3B.

C.

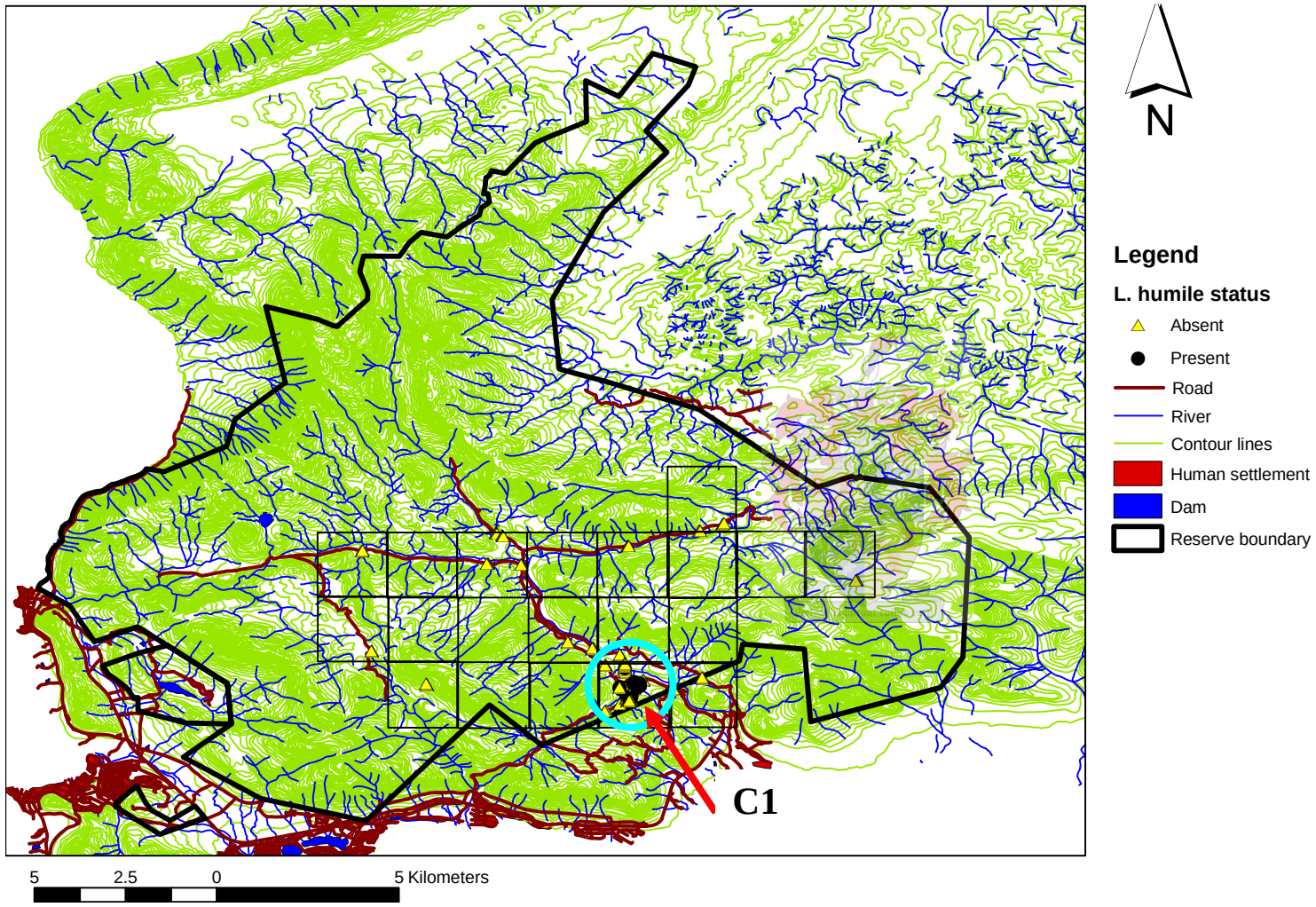

N
Legend
L. humile status
Absent
Present
Road
River
Contour lines
Human settlement
Dam
Reserve boundary
C1
5
2.5
0
5 Kilometers

Fig. 3C.

Fig. 3. Distribution of the Argentine ant at **A**. Helderberg Nature Reserve, **B**. Jonkershoek Nature Reserve, and **C**. Kogelberg Biosphere Reserve. Jonkershoek Nature Reserve (JNR) is part of the greater Hottentots-Hollands Nature Reserve, therefore for the purpose of this study only the area forming JNR was mapped. Grid cells indicate areas sampled for the presence/absence of the Argentine ant. Absence and presences of the Argentine ant are indicated by open triangles and closed circles respectively. A1, B1 and C1 = entrances to protected areas; B2 = Fire look-out station; B3 = Swartboskloof valley; B4 = Witbrug. Circled area on Fig. 3C = Oudebosch. Note differences in map scales.

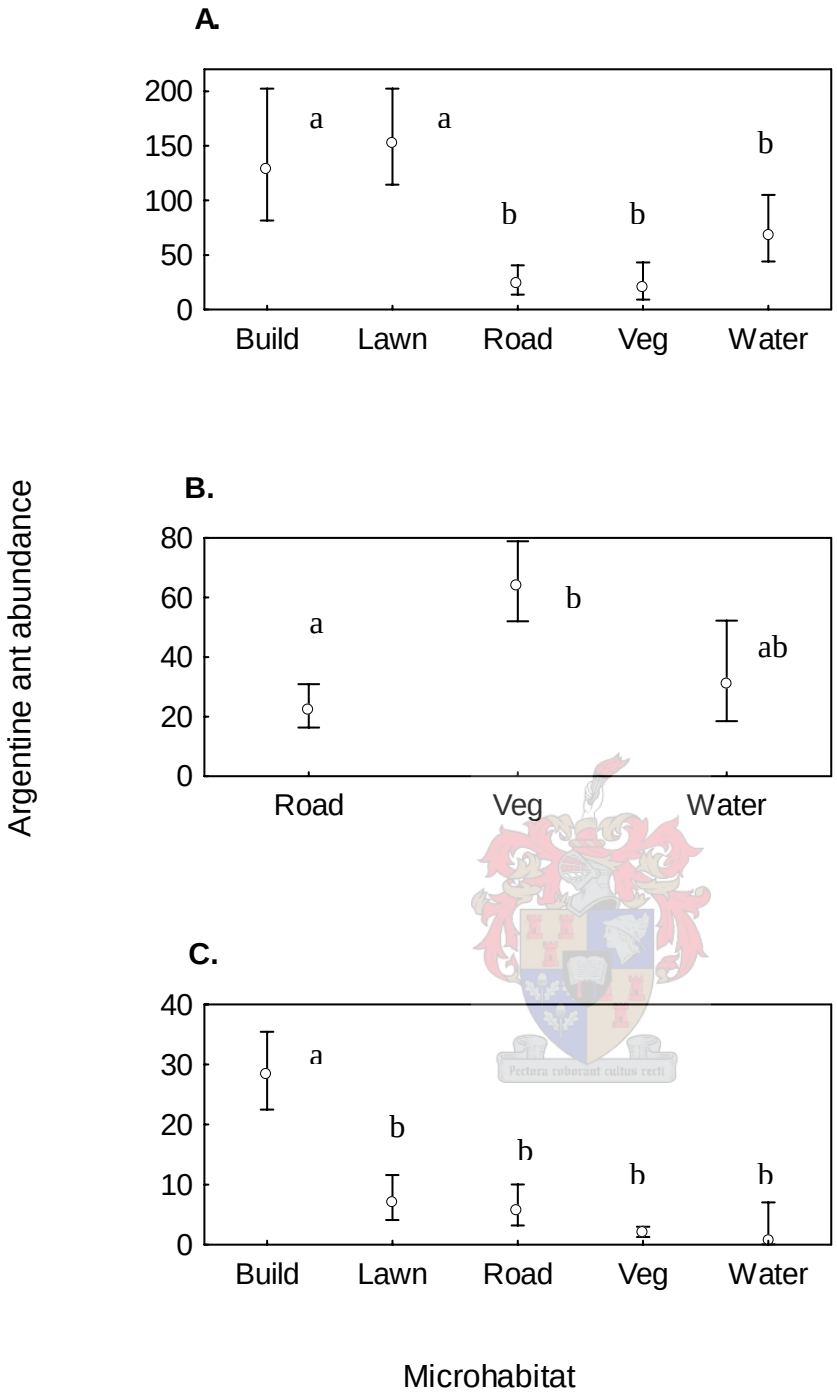


Fig. 4a. Mean (± S.E.) Argentine ant abundances at various microhabitats at **A**. Helderberg Nature Reserve, **B**. Jonkershoek Nature Reserve, and **C**. Kogelberg Biosphere Reserve. Different letters indicate significant differences between means at $p < 0.05$. Build = buildings, veg = vegetation, and water = adjacent to waterbodies.

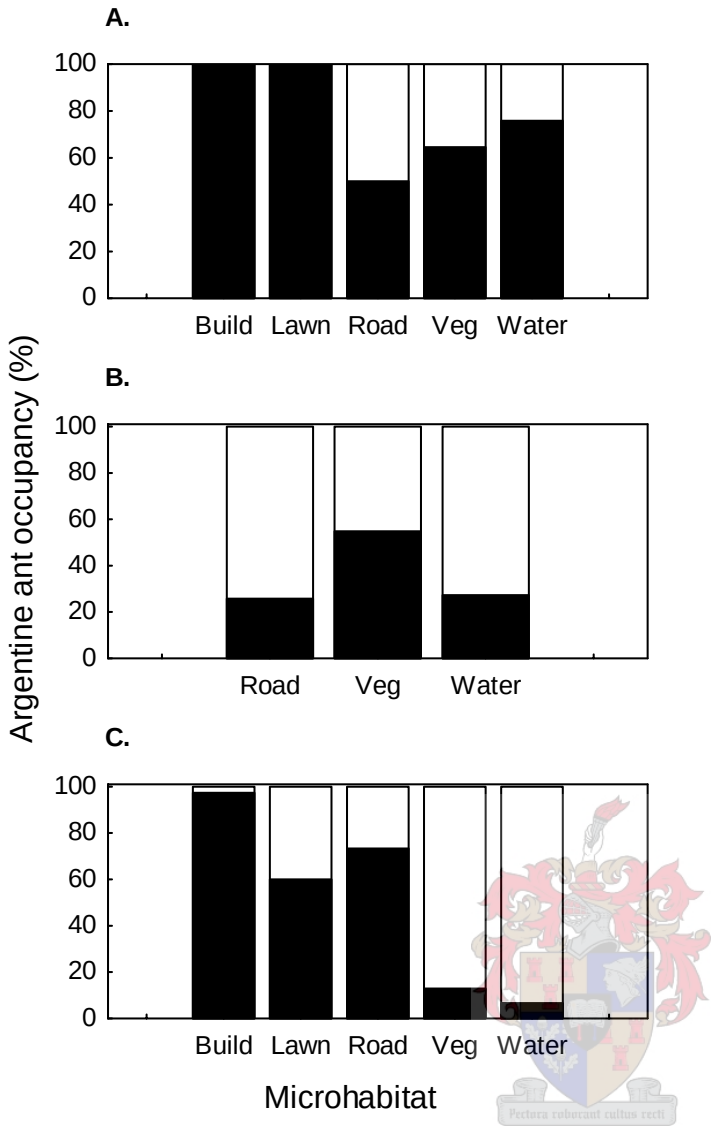


Fig. 4b. Percentage occupancies (black bars) of the Argentine ant at various microhabitats at **A.** Helderberg Nature Reserve, **B.** Jonkershoek Nature Reserve, and **C.** Kogelberg Biosphere Reserve. Build = buildings, water = adjacent to waterbodies, and veg = vegetation.

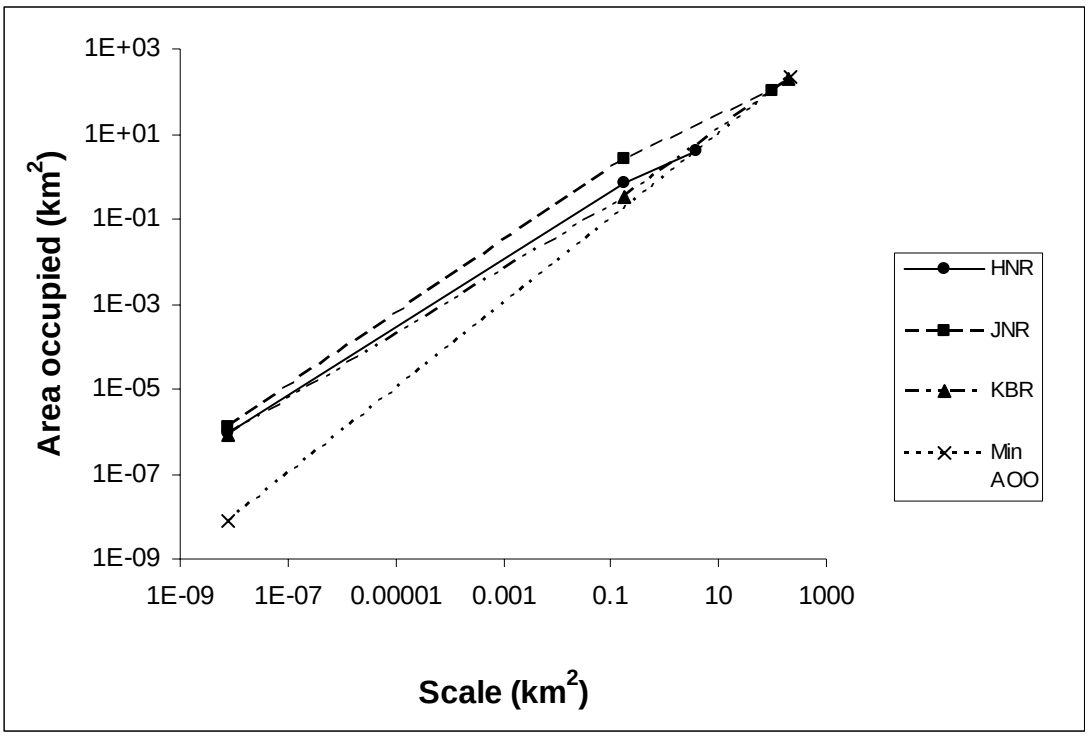


Fig. 5. Scale-area curves for the distribution of the Argentine ant in three Protected Areas. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, and KBR = Kogelberg Biosphere Reserve. Min AOO = minimum area of occupancy (i.e. when only one unit is occupied out of all potential units at that scale).

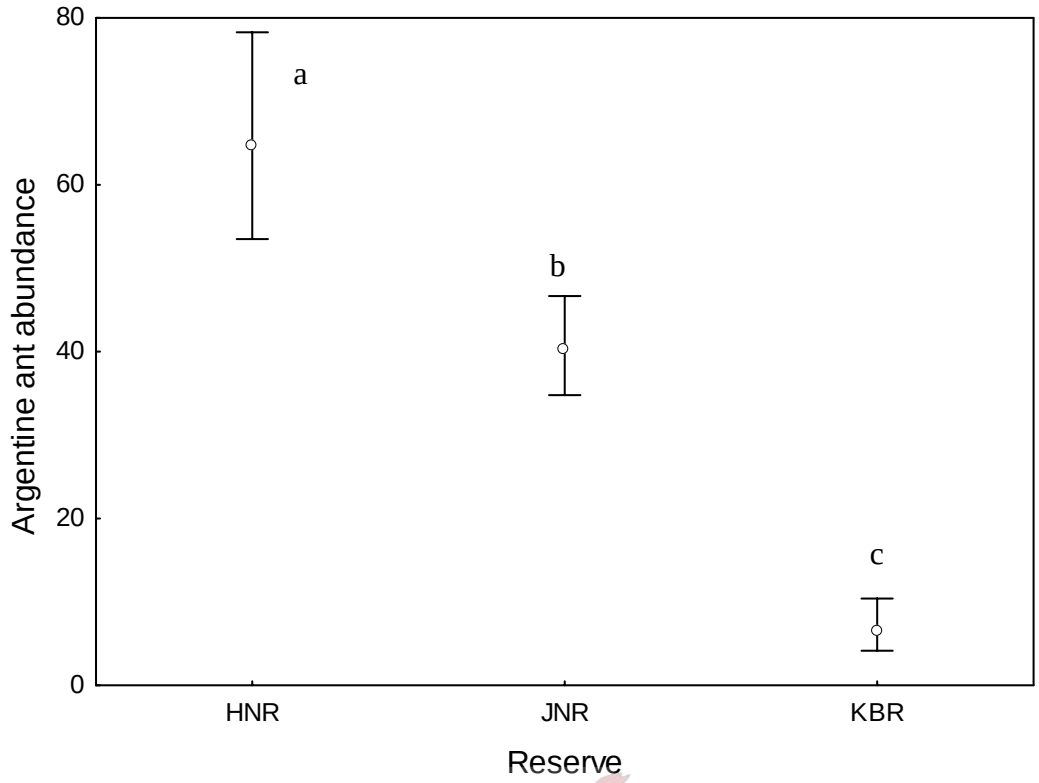
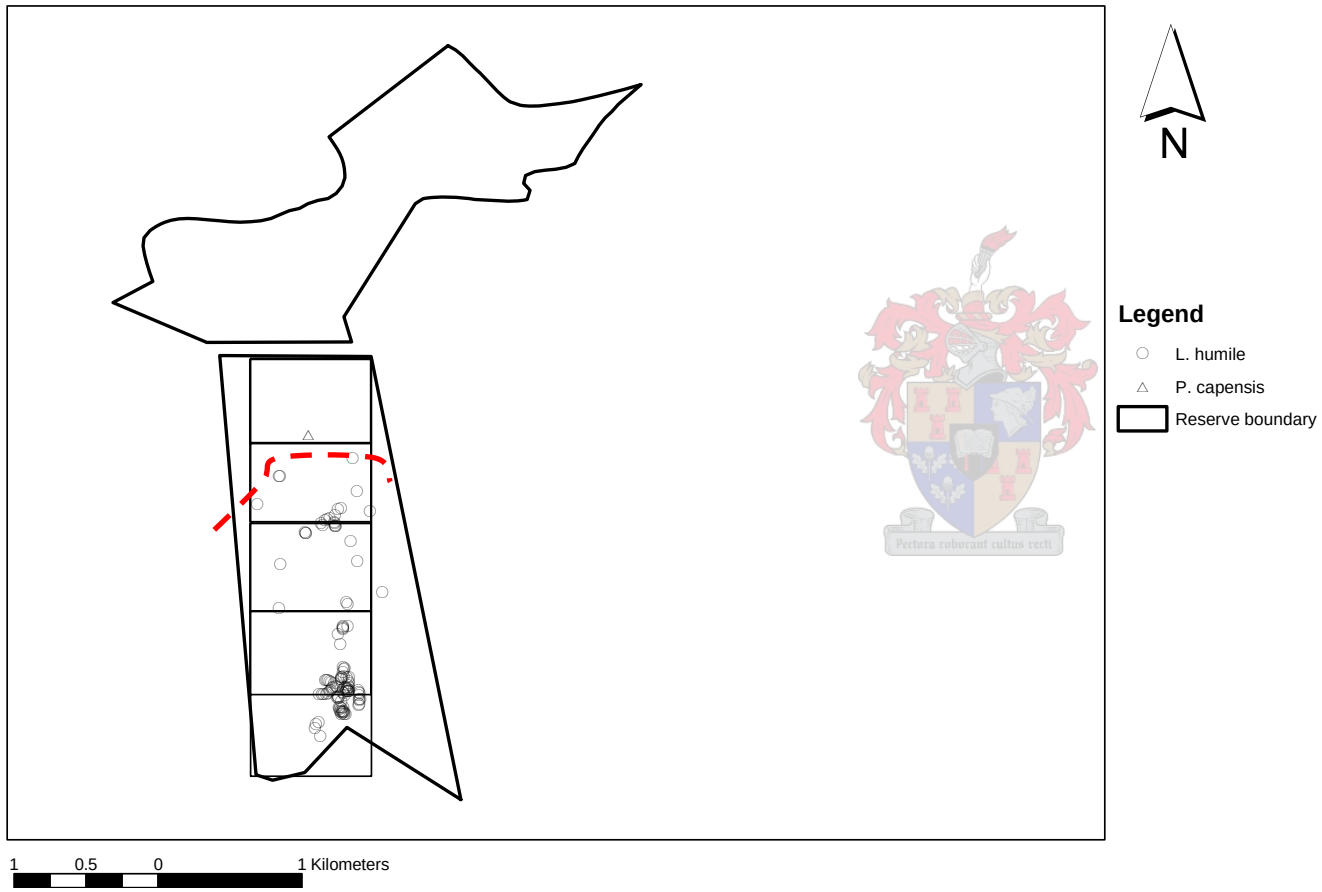


Fig. 6. Mean (± S.E.) Argentine ant abundances at bait stations in three Protected Areas. Different letters indicate significant differences between means at $p < 0.05$. HNR = Helderberg Nature Reserve, JNR = Jonkershoek Nature Reserve, and KBR = Kogelberg Biosphere Reserve.

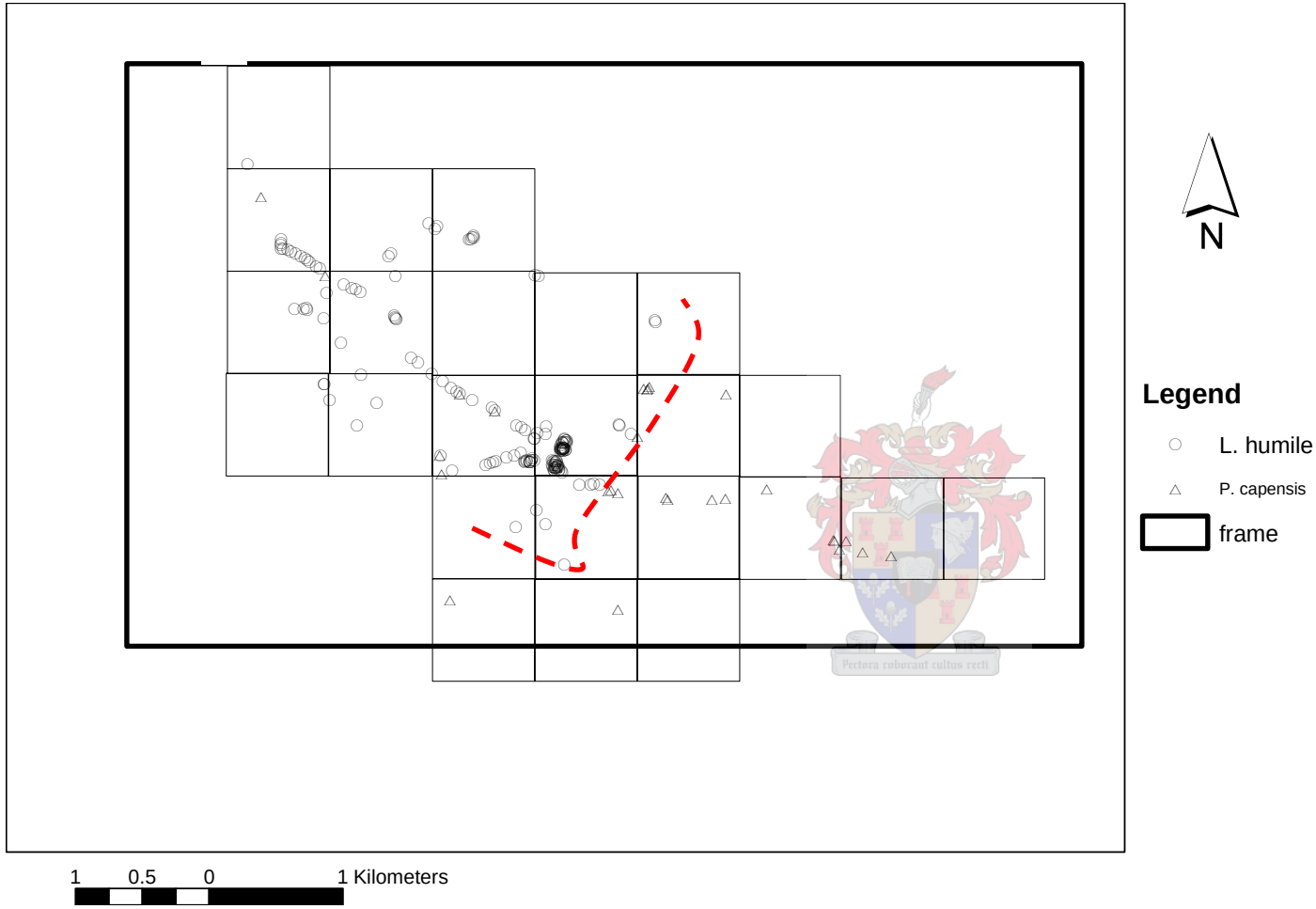
Appendix 1. Distribution of the Argentine ant and *Pheidole capensis*, without map layers, at **A.** Helderberg Nature Reserve, **B.** Jonkershoek Nature Reserve and **C.** Kogelberg Biosphere Reserve. Dotted lines indicate the approximate edge between invaded and uninvaded areas (invasion front).

A.



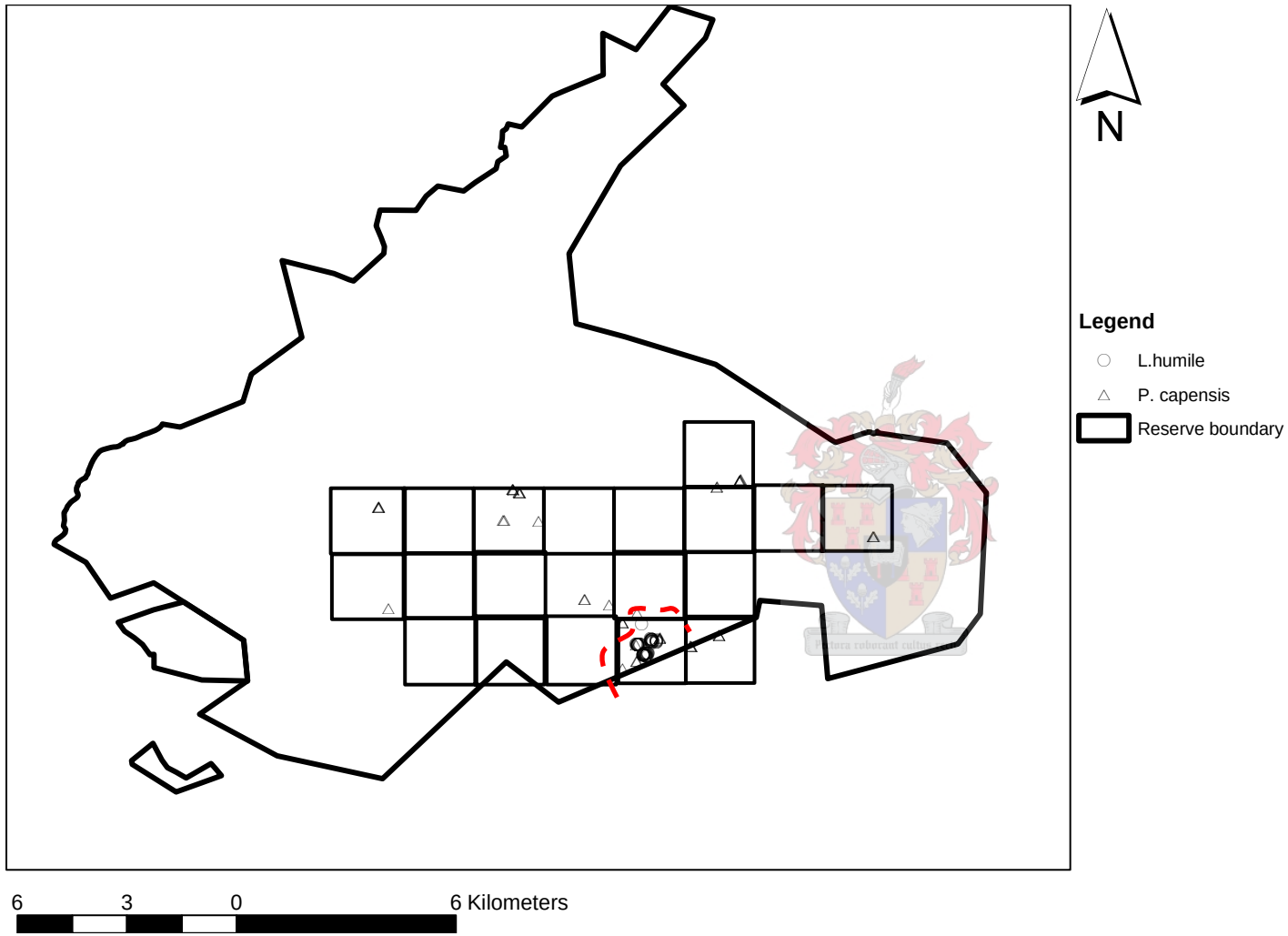
Appendix 1.A

B.



Appendix 1.B

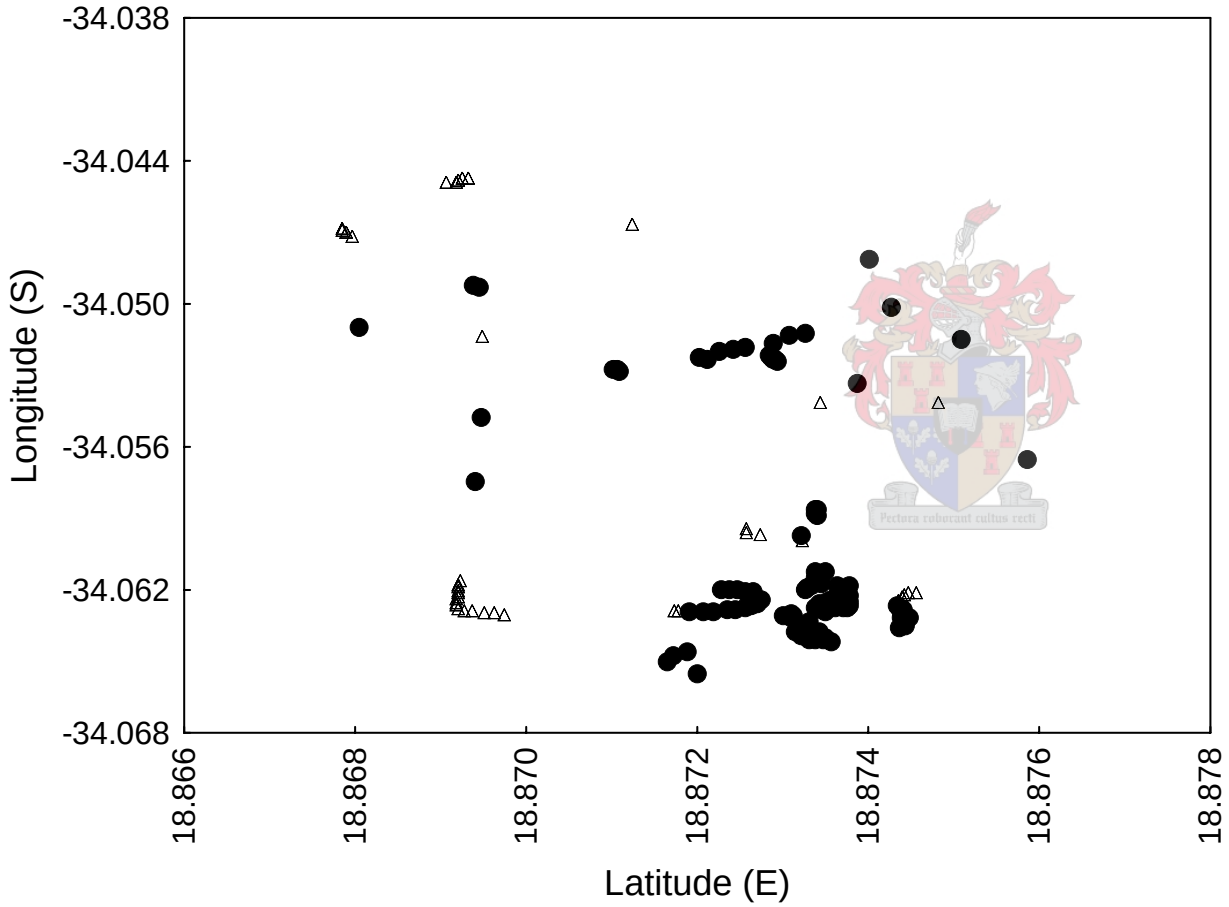
C.



Appendix 1.C.

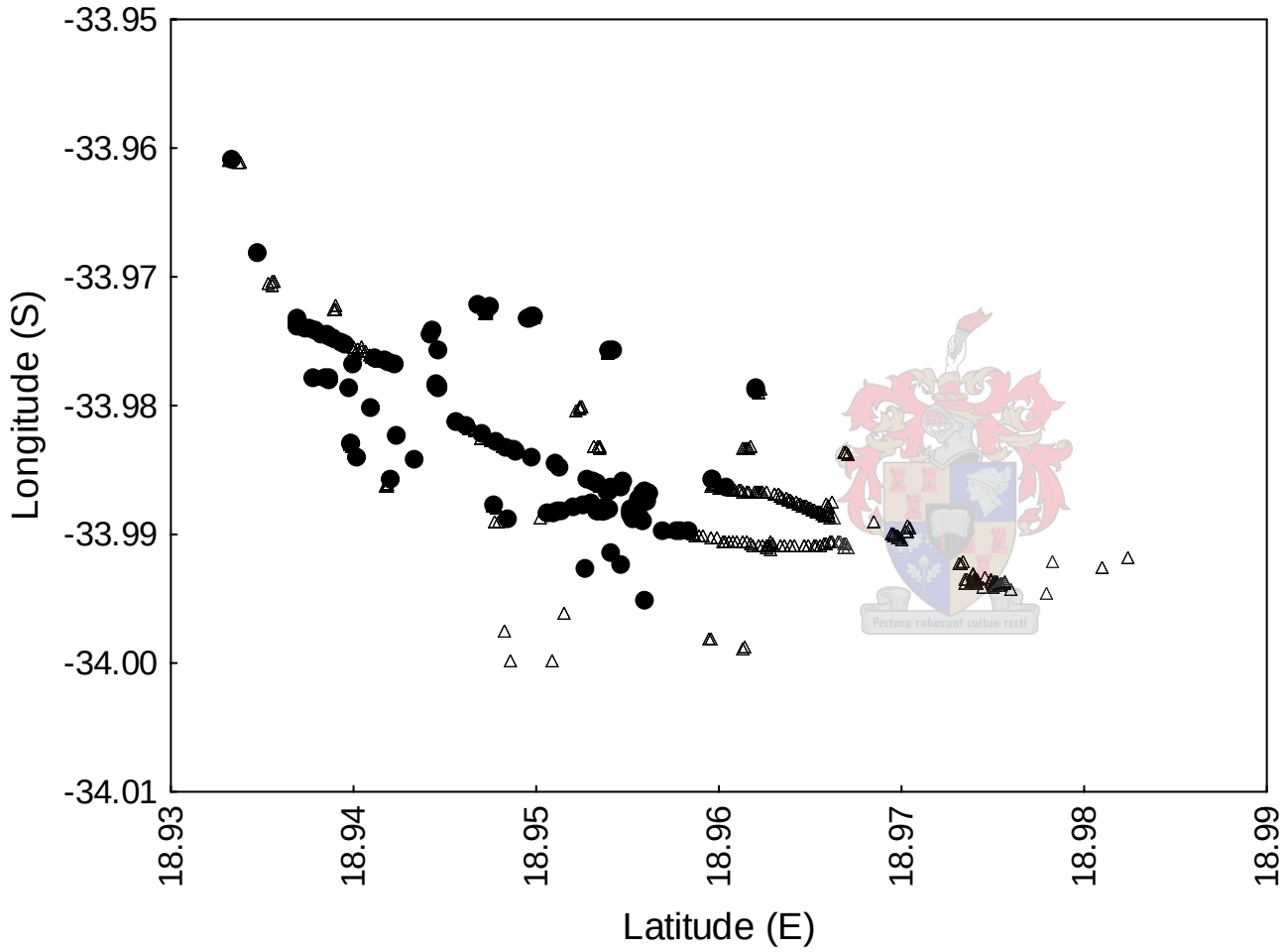
Appendix 2. Plots of the distribution of the Argentine ant at **A.** Helderberg Nature Reserve, **B.** Jonkershoek Nature Reserve, and **C.** Kogelberg Biosphere Reserve. Filled circles = presence, open triangles = absences.

A.



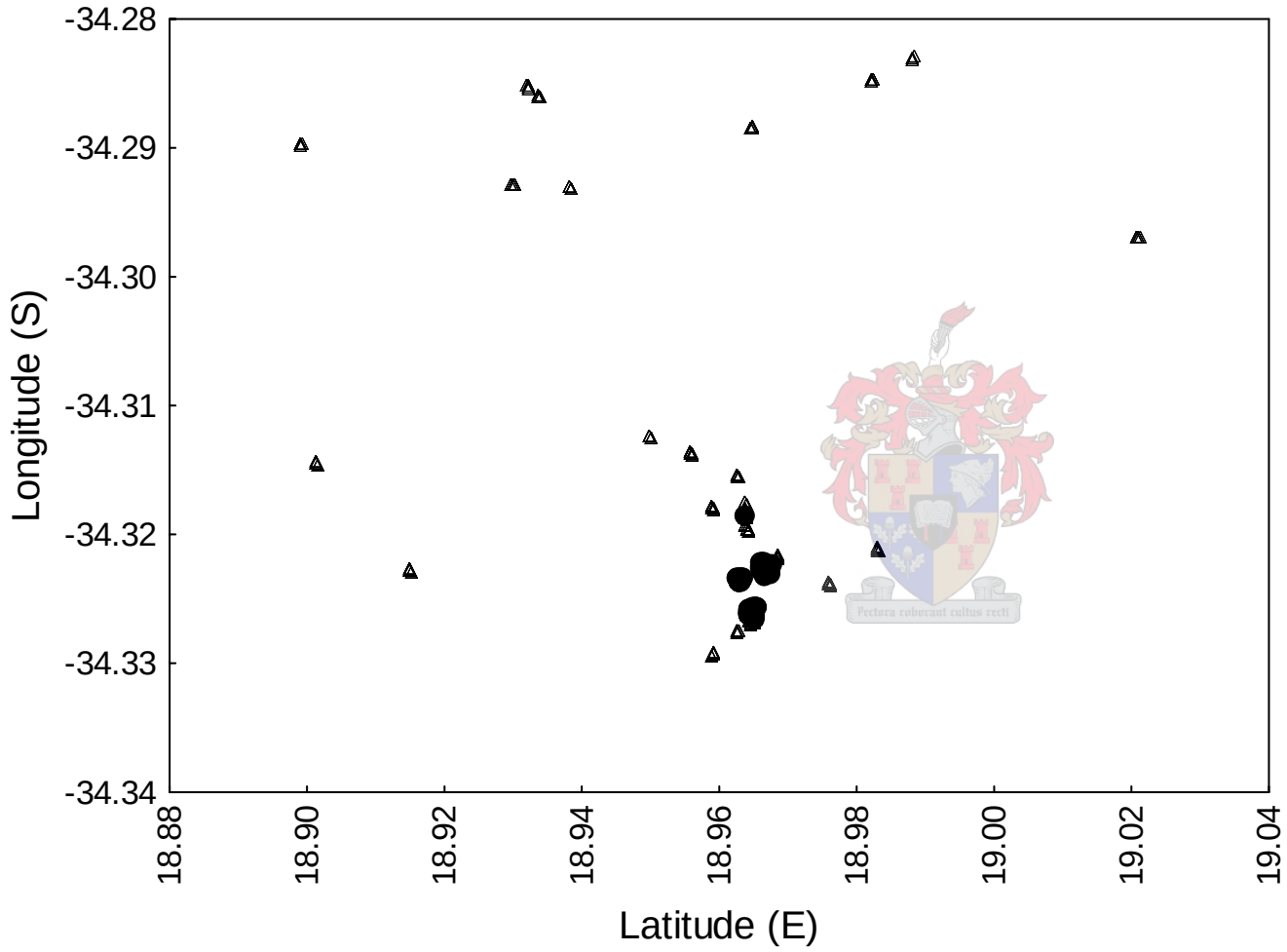
Appendix 2.A.

B.



Appendix 2.B.

C.



Appendix 2.C.

CHAPTER 4

Distributional extent and range expansion of the Argentine ant in South Africa

INTRODUCTION

Invasive ants are amongst the most ecologically damaging taxa in the world (Vega & Rust 2001; Pimental *et al*. 2001). Of all invasive ant species, the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae) has received the most attention worldwide (Lowe *et al*. 2000). This species is native to Argentina (South America), and has been introduced to six continents, except Antarctica, and many oceanic islands (Suarez *et al*. 2001). In many cases, invasion of natural habitats by the Argentine ant results in changes in the biodiversity and functioning of ecological systems (White *et al*. 2006), i.e. the displacement of native ants in natural areas (Erickson 1971; Ward 1987; Human & Gordon 1996; Holway 1999), the reduction in abundance of other arthropods (Cole *et al*. 1992), and the disruption of ant-plant mutualisms (Bond & Slingsby 1984; Christian 2001).

The Argentine ant is mainly transported around the globe through human activities, especially international trade (Jenkins 1996; McGlynn 1999). Characteristics of this tramp species make it readily carried around unintentionally (i.e. it prefers areas close to humans, with high anthropogenic disturbances and also forms supercolonies (Hölldobler & Wilson 1990; Passera 1994). Most invasive organisms, including the Argentine ant, are carried as stowaways in ships, planes, delivery trucks, shipping containers and packaging materials (Jenkins 1996). For example, in the Vanuatu Islands (Southwest Pacific), human transportation was found to be the principal cause of the spread of the invasive ant, *Wasmannia auropunctata* (Jourdan *et al*. 2002). In addition to human-mediated jump dispersal, Argentine ants are also able to spread naturally through budding of the nest (Ward *et al*. 2005). During nest budding, few Argentine ant workers, together with one or more queens, relocate to form a new nest in a favourable environment (Markin 1970a; Heller & Gordon 2006). In a laboratory experiment, Hee *et al*. (2000) showed that Argentine ants only require as few as 10 individual workers and one queen to establish a new colony. Thus, Argentine ant queens cannot survive and establish a successful colony

without workers, and vice versa (Hee *et al*. 2000). The natural rate of expansion (through nest budding) for the Argentine ant has been shown to be very slow (approximately 100 m/year) (Erickson 1971; Holway 1995). However, long distance dispersal of the Argentine ant along rivers and floodplains has also been reported (Ward 1987; Holway 1998).

Abiotic factors have been shown to play a large role in influencing the distribution of the Argentine ant (Human & Gordon 1996; Human *et al*. 1998; Holway *et al*. 2002a; Menke & Holway 2006). The distribution and spread of the Argentine ant may be limited by the shortage of moisture (Holway *et al*. 2002b; Menke & Holway 2006) and also by high temperatures (optimal temperature range for the Argentine ant is usually between 15-30 °C) (Markin 1970b; Human *et al*. 1998; Witt & Giliomee 1999; Thomas & Holway 2005). Thus, activities such as watering of lawns may facilitate invasion by the Argentine ant near human habitation, while rainfall and fog drip may influence it in natural areas (DiGirolamo & Fox 2006). However, biotic factors, i.e. interaction between the Argentine ant and native ants, may sometimes combine with abiotic stress, i.e. lack of moisture, to limit the spread of the Argentine ant into uninvaded communities (Holway *et al*. 2002b; Thomas & Holway 2005).

The Argentine ant was first recorded in South Africa in 1901 in the Stellenbosch area, Western Cape Province (WCP) (Prins *et al*. 1990). To date, the extent of the Argentine ant invasion throughout South Africa since introduction has not been quantified, although the species is considered to occur broadly in urban areas across South Africa. These invaded urban areas are also potential sources of introduction into nearby natural areas (Carpintero *et al*. 2003), as well as to other parts of the country through human-mediated jump dispersal, and over short distances via natural range expansion. Many parts of South Africa have a non-Mediterranean climate, thus making these areas potentially less vulnerable to invasion by the Argentine ant. However, a study conducted by Roura-Pascual *et al*. (2004) showed that, based on climate data modeling, the non-Mediterranean areas of South Africa are climatically suitable to the Argentine ant and are likely to be invaded. Moreover, suitable microhabitats such as increased moisture levels created in urban areas across the country (South Africa) could also promote the successful establishment of the Argentine ant in climate zones where it would otherwise

not readily survive (Holway *et al*. 2002a). According to the prediction made by Roura-Pascual *et al*. (2004), vulnerable areas include the Cape Peninsula, Eastern Cape, Free State and Gauteng Provinces. Hartley *et al*. (2006) suggested that environmental factors such as temperature and rainfall are likely to play an important role in setting broad-scale limits for the establishment of the Argentine ant, i.e. it is most likely to occur in areas where the mean daily temperature in winter is 7-14 °C and the maximum daily temperature during the hottest month is 19-30 °C on average. In general, the predictions made by Hartley *et al*. (2006) on the potential distribution range of the Argentine ant worldwide were consistent with that of Roura-Pascual *et al*. (2004). Although the prevalence of the Argentine ant is predicted to be high in South African urban areas, it has never been quantified.

The aim of this study was thus to quantify the distribution of the Argentine ant in South Africa, focusing on urban areas and along roadsides, i.e. those areas where it is most likely to be found. The following hypotheses were tested. (1) The Argentine ant has spread to many urban areas of South Africa outside the Mediterranean regions of the Western Cape Province since its introduction. (2) The Argentine ant is associated with human settlements across South Africa, i.e. it is found in houses and human-modified landscapes. In addition, the prevalence of other ant species found in urban areas and along roadsides in South Africa was assessed. (3) There is evidence of range expansion by the Argentine ant since the last, more limited (to the Western Cape Province), assessment of its distribution conducted between 1983 and 1984. (4) The existence of distributional discontinuities, i.e. the separation of invaded areas by absence records, in the distribution of the Argentine ant in South Africa was used to provide evidence of range expansion by the species via human-mediated jump dispersal.

MATERIALS AND METHOD

Data collection

Data were obtained by collating locality records from previous literature, museum records (obtained from Iziko Museum of South Africa, Cape Town) and samples

collected in this study. A literature search for ant studies in South Africa was conducted, and this search produced 13 relevant studies. These publications were reviewed to assess if the Argentine ant was recorded during sampling (see Appendix 1 for a list of these publications). Thus, the ant species lists in these studies were examined, and if the Argentine ant was not recorded in the list, it was presumed absent for the area where the study was conducted, and was confirmed present if listed. This was done to establish the presence and absence of the Argentine ant from around the country, although literature information largely gives presences and not absences of species.

To collect information on the distribution of the Argentine ant, sampling kits (consisting of an envelope, which contained a 1.5 ml epindof tube half-filled with 100 % ethanol) were distributed during February 2005 among students and staff of the University of Stellenbosch, and also to community members of Stellenbosch and neighbouring towns. People were asked to collect ant samples from their homes (houses and gardens) and any urban areas across the country. Samples were collected from urban areas to maximize chances of finding the Argentine ant, as it is widely known that this species prefers areas with high anthropogenic disturbances (Passera 1994; Carpintero *et al*. 2003). An information sheet containing a short background on the Argentine ant, as well as instructions to the collector, was included in the envelope (Appendix 2), and the envelope contained a label with particulars required from the collector (Appendix 3).

Targeted field trips were also conducted to those parts of the country where there were gaps in the distributional data available, including Free State, Limpopo, Mpumalanga and Northern Cape Provinces.

All samples obtained were examined under a microscope for the presence of the Argentine ant. Other native ant species collected were also identified, in most cases to genus level and in some cases to species level (identifications confirmed by Dr. C.L. Parr, CSIRO, Australia). Voucher specimens are kept at the DST-NRF Center for Invasion Biology, University of Stellenbosch, South Africa.

Data analyses

Distribution and range expansion

The occupancy status of the Argentine ant (presence and absence) across the country was plotted on a map using ArcGIS version 8. Because most samples provided did not have the specific GPS coordinates, street addresses provided were used to determine the locality from which the samples were collected. Geographic Information Systems (GIS) data was obtained from Surveys and Mapping, Mowbray (Cape Town, South Africa), and additional data was also obtained from the Department of Geography, University of Stellenbosch. The distribution map of the Argentine ant in South Africa was subjectively divided into invaded and uninvaded areas, based on a combination of the presence and absence distribution data obtained from across the country. This grouping into areas of presence and absence forms a hypothetical basis for testing for possible differences in genetic population structure across the country. The population perimeters were estimated based on distributional discontinuities. Thus, invaded areas uninterrupted by absence records, that were also geographically closer to each other than to uninvaded areas, were considered as one population. To estimate the average distance between neighbouring invaded areas (i.e. distributional discontinuities), the relative distance between the invaded areas was measured (in km). Only invaded areas separated by uninvaded areas (absence records) were included in the analysis. The analysis was performed in STATISTICA for windows, version 7. The extent of occurrence of the Argentine ant in South Africa was determined using Garmin MapSource version 6.10.2.

Range expansion of the Argentine ant in the Western Cape Province since the survey by De Kock (1990) (between 1983 and 1984) was assessed. This was done by comparing De Kock's absence records with records from the current study. Thus, if the Argentine ant was absent from an area during sampling by De Kock in 1983, and was now present in the same area during current sampling, this was then considered as evidence for range expansion.

Microhabitat preference

To test for differences in Argentine ant occupancy across various microhabitats, i.e. houses, gardens and along roadsides in urban areas of South Africa, Chi-square analysis was used (Zar 1984). Because some samples provided did not specify the microhabitat from which the ants were collected, these samples were grouped into the microhabitat "other".

Other ant species

The relative prevalence (number of occurrences) of other ant species in various human-influenced microhabitats in different provinces was calculated. These results were compared with the assessment of Prins *et al*. (1990).

RESULTS

Distribution and range expansion

Since the first official record of the Argentine ant in South Africa in 1901, there has been a substantial increase in the number of Argentine ant records for the country (Fig.1). South Africa covers a total surface area of 1 260 150 km^2 divided into nine provinces. Results of this study showed that almost half of this area (596 235 km^2, including six of nine provinces) encompasses sites occupied by the Argentine ant (Fig. 2). The Argentine ant was found in and around major towns in each province, and most of these invaded towns are accessible by national roads (Fig. 2), although these results are biased because most of the samples in this study were collected from urban areas. The observed extent of occurrence of the Argentine ant in South Africa is thus currently 47 % of the country's land surface area (Fig. 3). However, based on the collated data and samples collected in this study, the prevalence of the Argentine ant across all samples in the country was 34.7 % (Table 1). Five invaded and four uninvaded areas across the country were delineated

(Fig. 4). The Fynbos biome had the highest number of areas occupied by the Argentine ant, while the Savanna biome had the fewest invaded areas (Fig. 5). However, this result may be biased by the collection effort at each biome. Average gaps, or distributional discontinuities between invaded areas of greater than 200 km were found (210.65 ± 25.06 km; N = 18). For example, the distance between Lutzville and Calvinia, and also between Calvinia and Upington etc. (see Fig 2). There were significant differences in the prevalence of the Argentine ant between microhabitats across the country (d.f. = 3, X^2 = 31.35, $p < 0.001$). Houses, followed by gardens, had the highest Argentine ant percentage prevalence across the country compared to the prevalence along roadsides (Table 1).

During the current study, the Argentine ant was recorded from three areas within the WCP where it was absent during previous sampling by De Kock (1990), i.e. Clanwilliam, Malmesbury and Heidelberg (points A, B and C respectively - Fig. 6) providing evidence for range expansion in this province.

Other ant species

In total, 33 other ant species (excluding the Argentine ant) were collected from across South Africa in this study (Table 2). *Pheidole megacephala* was more widespread across the country than the Argentine ant, i.e. recorded from seven provinces while the Argentine ant was recorded from five provinces (Table 2). *Pheidole megacephala* was found mainly in areas where the Argentine ant was absent (Fig. 7). *Lepisiota incisa*, followed by *Technomyrmex albipes*, were the third and forth most prevalent native ant species countrywide, respectively (Table 3). *Tetramorium quadrispinosum*, a widespread native ant species, was found in five provinces, although only in 15 samples (Table 2). Almost 40 % of the species were each collected from only one province (Table 2), and 60 % of the species had less than 1 % total prevalence in all the microhabitats across the country (Table 3). More than half of the total ant species collected in this study were each found in less than 5 samples (Table 2).

DISCUSSION

Distribution and range expansion

This is the first study quantifying the distribution of the Argentine ant throughout South Africa. Results of this study showed that since the first record of the Argentine ant in South Africa in 1901, this species has successfully invaded six provinces, including those areas outside the Mediterranean climate zone (the Western Cape Province is the only province in the country with a Mediterranean climate). Thus, this study demonstrated that Mediterranean climate does not play a major role in limiting the establishment and spread of the Argentine ant in South Africa. However, in this study sampling was done in urban areas and along roadsides, and thus the modified climate and local habitat conditions such as food availability, heating and irrigation in these areas could make even these non-Mediterranean provinces suitable for the establishment of the Argentine ant (Espadaler & Gómez 2003). Water runoff along roadsides may also provide the necessary moisture required for the establishment of the Argentine ant (Holway *et al*. 2002a). Almost half of the country's land surface area based on sampling in urban areas is occupied by the Argentine ant. The distribution range of the Argentine ant in this study was consistent with that predicted by Roura-Pascual *et al*. (2004). Thus, results of this study confirmed that those areas within South Africa, which Roura-Pascual *et al*. (2004) (see Fig. 2a) predicted to be vulnerable to the Argentine ant invasion, were already invaded by this species (see Fig. 3). Furthermore, some areas within the Northern Cape Province, i.e. Upington, Prieska and Kuruman, which were not predicted by Roura-Pascual *et al*. (2004) to be vulnerable to invasion, were also invaded by the Argentine ant.

There were distributional discontinuities in the distribution pattern of the Argentine ant throughout South Africa. The average distance between invaded areas separated by known absences was greater than 200 km. This distance is much larger than would be expected given the general rate of natural diffusion for Argentine ants (around 100 m/year) (Crowell 1968; Erickson 1971; Holway 1995). Thus, this study provides strong evidence that new introductions of the Argentine ant to various parts of South Africa are

occurring virtually exclusively via human-mediated jump dispersal, rather than naturally via nest diffusion. Argentine ants do not spread naturally over long distances, due to lack of flight in queens (Holway & Suarez 2004). However, it is also possible that since Argentine ants form supercolonies (Passera 1994), they may also spread into other areas via nest budding, especially between neighbouring towns. In Davis (California), Holway (1998) found that the rate of spread of the Argentine ant was approximately 16 m/year. However, in northern San Mateo County (California), Sanders *et al*. (2001) found that the rate of spread of the Argentine ant can be much quicker than previously found (100 – 500 m/year), and that this rate may vary between seasons.

Human-mediated jump dispersal (HMD) plays an important role in the transport of the Argentine ant over long distances (Holway 1995; Suarez *et al*. 2001), and this process has carried the Argentine ant to all the continents around the world, except Antarctica (Hölldobler & Wilson 1990). However, HMD can also play a role over relatively short distances, e.g. within South African urban areas (Suarez *et al*. 2001; Ward *et al*. 2005). Human-mediated jump dispersal may also lead to the formation of many new populations of Argentine ants that would otherwise not occur naturally (Ward *et al*. 2005). The widespread establishment of many independent Argentine ant populations via HMD has important implications for accelerating its range expansion at both small and large scales (Moody & Mack 1988).

In this study, the Argentine ant was recorded from areas in the WCP (i.e. Clanwilliam, Malmesbury and Heidelberg) where it was absent during previous survey (between 1983 and 1984) by De Kock (1990). This provides evidence that there has been successful range expansion in the distribution of the Argentine ant over the last 22 years. This range expansion could also be the result of human mediation. The Argentine ant was associated with houses and gardens throughout the country as opposed to roadsides, and this result is consistent with findings of studies conducted elsewhere in the world (Ward 1987; Carpintero *et al*. 2003).

Other ant species

Several other ant species (in addition to the Argentine ant) were collected from around the country in this study. Prins *et al*. (1990) identified four most important pest ant species in South Africa: the Argentine ant (*Linepithema humile*), the brown house ant (also known as the big-headed ant or brown coastal ant) (*Pheidole megacephala*), the common pugnaceous ant (*Anoplolepis custodiens*) and the black pugnaceous ant (*Anoplolepis steingroeveri*) (*sensu* Prins *et al*. (1990) for a list of the common pest ant species in Southern Africa).

The brown house ant was the second most prevalent ant species in this study, and was collected from more provinces than the Argentine ant. This species is also a tramp ant species just like the Argentine ant, and although it is indigenous to South Africa, it is a major pest in homes (it is a nuisance to humans, and may cause damage to food crops) (Prins *et al*. 1990), and also an invasive ant elsewhere in the world. Prins *et al*. (1990) classified *P. megacephala* as one of the four most important pest ant species in bio-control and houses in South Africa. However, results of this study showed that this species was more prevalent along roadsides than in houses and gardens, and was only collected from areas where the Argentine ant was absent. Although this result could be biased by the collection effort at each habitat. The brown house ant and the Argentine ant share similar characteristics (Passera 1994) and will thus compete directly with each other for the same resources when occurring in the same area.

Technomyrmex albipes, another worldwide tramp ant species and classified by Prins *et al*. (1990) as a major bio-control and household pest, was also a widespread and prevalent species in this study. This species was more common in houses than in gardens and along roadsides.

Five *Anoplolepis* species, including *A. custodiens*, were collected in this study. Prins *et al*. (1990) classified two species in this genus, *Anoplolepis steingroeveri* and *Anoplolepis custodiens*, as two of the four major pest ants, particularly in bio-control, in South Africa. However, in this study, *A. custodiens* was collected in very few samples, thus making it difficult to make any conclusions regarding its pest status. All the five *Anoplolepis*

species collected in this study had very low prevalence, with a combined total for all five species of 6.3 %.

Some species within the *Tetramorium* and *Monomorium* genera are widespread in Southern Africa, but are not pests in urban and agricultural areas (Prins *et al*. 1990). In this study six *Tetramorium* species, including *T. quadrispinosum* were collected. *Tetramorium* sp. 2 was the most widespread and most prevalent, followed by *T. quadrispinosum*. *Tetramorium quadrispinosum* and the other four *Tetramorium* species were not collected from houses (only *Tetramorium* sp. 2 was collected from inside the house), thus these results confirmed that although species within the *Tetramorium* genus are common across the country, they do not cause problems in homes. In the Cape Peninsula, *T. quadrispinosum* is common in urban areas, but it rarely enters into houses (Prins *et al*. 1990). Only one *Monomorium* species was collected in this study (from one sample, along the roadside), also confirming it is not a problem ant species.

The seed harvesting ant, *Messor capensis*, is a major pest in pasture (Prins *et al*. 1990). In this study, this species was not common, and was only collected from gardens and along roadsides, with equal prevalence at both habitats. Two other *Messor* species were also collected, but only from one sample each.

Four *Camponotus* species, including *C. fulvopilosus*, were collected from various habitats in this study, i.e. house, garden and along roadsides. Species in this genus are considered to be of minor importance as pests in bio-control, but can damage the leaves and growing tips of young trees (Prins *et al*. 1990).

The genus *Crematogaster* is a major pest in bio-control, and species in this genus nest in pre-existing cavities made by wood-boring beetles (Prins *et al*. 1990). In this study, only one *Crematogaster* species was collected from the garden, found in only two samples.

Lepisiota incisa was one of the most widespread, and the third most prevalent ant species in this study. This species was collected from all the various habitats, however, its pest status was not determined by Prins *et al*. (1990).

The Argentine ant was the most prevalent ant species in this study, and often, no other native ant species were found in the same sample with it (although this is biased by the short temporal snapshot sampling method). This species was therefore the most dominant

ant species in invaded urban areas, after probably displacing the native ant species that were once present before invasion. Thus, the increase in the distribution range of the Argentine ant could lead to the displacement of more native ant species throughout South Africa. It was not clear from this study why some areas of South Africa remain uninvaded by the Argentine ant, particularly within the Mediterranean WCP. However, it is possible that some of these areas are already invaded by the Argentine ant, but remains undetected (Roura-Pascual *et al*. 2004). There are two other possible explanations to this: (1) the Argentine ant has never been introduced into these areas, or (2) the Argentine ant has been introduced to these areas, but fail to establish there due to competition or biotic resistance from native ant species. Furthermore, previous studies conducted elsewhere in the world have demonstrated that for Argentine ants to establish successfully in a new area, their colony size must be 5-10 times greater than that of the native ants (Walters & Mackay 2005). In addition, introduced Argentine ant populations should contain a complete nest, i.e. both workers and at least one queen, because an Argentine ant colony containing only workers can not survive without the queen, and vice versa (Hee *et al*. 2000).

The Argentine ant is well established in South Africa, and evidence suggests that ongoing increases in its extent of occurrence are human-mediated. Because the majority of samples in this study were collected in urban areas and along roadsides, no inferences can be made about the Argentine ant in natural areas. However, other studies suggest that it might not be present in natural areas outside the Western Cape Province. As has been shown elsewhere in the world, range expansion of the Argentine ant in South Africa could be significantly reduced by controlling and limiting the human-mediated establishment of new populations.

REFERENCES

ADDISON, P. & SAMWAYS, M.J. 2000. A survey of ants (Hymenoptera: Formicidae) that forage in vineyards in the Western Cape Province, South Africa. *African Entomology* **8**: 251-260.

BOND, W.J. & SLINGSBY, P. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorus Proteaceae. *Ecology* **65**: 1031-1037.

BOONZAAIER, C. 2006. *Conservation in human-influenced areas: epigaeic arthropods in the Cape Floristic Region lowlands*. MSc Thesis, University of Stellenboch, Stellenbosch.

BOTES, A., MCGEOCH, M.A., ROBERTSON, H.G., VAN NIEKERK, A., DAVIDS, H.P. & CHOWN, S.L. 2006. Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography* **33**: 71-90.

CARPINTERO, S., REYES-LÓPEZ, J. & ARIAS DE REYNA, L. 2003. Impact of human dwellings on the distribution of the exotic Argentine ant: a case study in the Doñana National Park, Spain. *Biological Conservation* **115**: 279-289.

CHRISTIAN, C.E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* **413**: 635-639.

COLE, F.R., MEDEIROS, A.C., LOOPE, L.L. & ZUEHLKE, W.W. 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology* **73**: 1313-1322.

CROWELL, K.L. 1968. Rates of competitive exclusion by the Argentine ant in Bermuda. *Ecology* **49**: 551-555.

DE KOCK, A.E. 1990. *The Argentine ant,* Iridomyrmex humilis *Mayr, indigenous ants and other epigaeic invertebrates of the fynbos in relation to fire and vegetation age*. MSc Thesis, University of Stellenboch, Stellenbosch.

DIGIROLAMO, L.A. & FOX, L.R. 2006. The influence of abiotic factors and temporal variation on local invasion patterns of the Argentine ant (*Linepithema humile*). *Biological Invasions* **8**: 125-135.

DONNELLY, D. & GILIOMEE, J.H. 1985. Community structure of epigaeic ants (Hymenoptera: Formicidae) in fynbos vegetation in the Jonkershoek valley. *Journal of the Entomological Society of Southern Africa* **48**: 247-257.

ERICKSON, J.M. 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. *Psyche* **78**: 257-266.

ESPADALER, X. & GÓMEZ, C. 2003. The Argentine ant, *Linepithema humile*, in the Iberian Peninsula. *Sociobiology* **42**: 187-192.

HARTLEY, S., HARRIS, R. & LESTER, P.J. 2006. Quantifying uncertainty in the potential distribution of an invasive species: climate and the Argentine ant. *Ecology Letters* **9**: 1068-1079.

HEE, J.J., HOLWAY, D.A., SUAREZ, A.V. & CASE, T.J. 2000. Role of propagule size in the success of incipient colonies of the invasive Argentine ant. *Conservation Biology* **14**: 559-563.

HELLER, N.E. & GORDON, D.M. 2006. Seasonal spatial dynamics and causes of nest movement in colonies of the invasive Argentine ant (*Linepithema humile*). *Ecological Entomology* **31**: 499-510.

HÖLLDOBLER, B. & WILSON, E.O. 1990. *The ants*. Harvard University Press, Cambridge, Massachusetts.

HOLWAY, D.A. 1995. Distribution of the Argentine ant (*Linepithema humile*) in Northern California. *Conservation Biology* **9**: 1634-1637.

HOLWAY, D.A. 1998. Factors governing rate of invasion: a natural experiment using Argentine ants. *Oecologia* **115**: 206-212.

HOLWAY, D.A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* **80**: 238-251.

HOLWAY, D.A., SUAREZ, A.V. & CASE, T.J. 2002a. Role of abiotic factors in governing susceptibility to invasion: A test with Argentine ants. *Ecology* **83**: 1610-1619.

HOLWAY, D.A., LACH, L., SUAREZ, A.V., TSUTSUI, N.D. & CASE, T.J. 2002b. The causes and consequences of ant invasions. *Annual Review of Ecological Systematics* **33**: 181-233.

HOLWAY, D.A. & SUAREZ, A.V. 2004. Colony-structure variation and interspecific competitive ability in the invasive Argentine ant. *Oecologia* **138**: 216-222.

HUMAN, K.G. & GORDON, D.M. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* **105**: 405-412.

JENKINS, P.T. 1996. Free trade and exotic species introductions. *Conservation Biology* **10**: 300-302.

JOURDAN, H., BONNET DE LARBOGNE, L. & CHAZEAU, J. 2002. The recent introduction of the Neotropical tramp ant Wasmannia auropunctata (Hymenoptera: Formicidae) into Vanuatu Archipelago (Southwest Pacific). *Sociobiology* **40**: 483-509.

LOWE, S., BROWNE, M., BOUDJELAS, S. & DE POORTER, M. 2000. 100 of the world's worst invasive alien: a selection from the Global Invasive Species Database. *The Invasive Species Specialist Group (ISSG), World Conservation Union (IUCN).*

MARKIN, G.P. 1970a. The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae), in Southern California. *Annals of the Entomological Society of America* **63**: 1238-1242.

MARKIN, G.P. 1970b. Foraging behaviour of the Argentine ant in a California citrus grove. *Journal of Economic Entomology* **63**: 740-744.

MCGLYNN, T.P. 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography* **25**: 535-548.

MENKE, S.B. & HOLWAY, D.A. 2006. Abiotic factors control invasion by Argentine ants at the community scale. *Journal of Animal Ecology* **75**: 368-376.

MOODY, M.E. & MACK, R.N. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* **25**: 1009-1021.

PARR, C.L., BOND, W.J. & ROBERTSON, H.G. 2002. A preliminary study of the effect of fire on ants (Formicidae) in South African savanna. *African Entomology* **10**: 101-111.

PARR, C.L., ROBERTSON, H.G., BIGGS, H.C. & CHOWN, S.L. 2004. Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology* **41**: 630-642.

PASSERA, L. 1994. Characteristics of tramp species. In: Williams, D.F. (Ed). *Exotic ants*: *biology, impact and control of introduced species*. 23-43. Westview Press, Colorado, USA.

PIMENTEL, D., MCNAIR, S., JANECKA, J., WIGHTMAN, J., SIMMONDS, C., O'CONNEL, C., WONG, E., RUSSEL, L., ZERN, J., AQUINO, T. & TSOMONDO, T. 2001. Economic and environmental threats of alien plant, animal and microbe invasions. *Agriculture, Ecosystems and Environment* **84**: 1-20.

PRINS, A.J., ROBERTSON, H.G. & PRINS, A. 1990. Pest ants in urban and agricultural areas of Southern Africa. In: Vander Meer, R.K., Jaffe, K, & Cedeno, A. (Eds). *Applied myrmecology*: *a world perspective*. 25-33. Westview Press, Colorado, USA.

ROURA-PASCUAL, N., SUAREZ, A.V., GÓMEZ, C. PONS, P., TOUYAMA, Y., WILD., A.L. & PETERSON, T. 2004. Geographical potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. *Proceedings of the Royal Society of London B.* **271**: 2527-2534.

RUTHERFORD, M.C. & WESTFALL, R.H. 1994. *Biomes of southern Africa: an objective characterization*. Memoirs of the Botanical Survey of South Africa. No. 63.

SANDERS, N.J., BARTON, K.E. & GORDON, D.M. 2001. Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. *Oecologia* : 123-130.

SUAREZ, A.V., HOLWAY, D.A. & CASE, T.J. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proceedings of the National Academy of Science* **98**: 1095-1100.

THOMAS, M.L. & HOLWAY, D.A. 2005. Condition-specific competition between invasive Argentine ants and Australian *Iridomyrmex*. *Journal of Animal Ecology* **74**: 532-542.

VAN HAMBURG, H., ANDERSEN, A.N. MEYER, W.J. & ROBERTSON, H.G. 2004. Ant community development on rehabilitated ash dams in the South African highveld. *Restoration Ecology* **12**: 552-558.

VEGA, S.Y. & RUST, M.K. 2001. The Argentine ant – a significant invasive species in agricultural, urban and natural environments. *Sociobiology* **37**: 3-25.

WALTERS, A.C. & MACKAY, D.A. 2005. Importance of large colony size for successful invasion by Argentine ants (Hymenoptera: Formicidae): evidence for biotic resistance by native ants. *Austral Ecology* **30**: 395-406.

WARD, P.S. 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. *Higardia* **55**: 1-16.

WARD, D.F., HARRIS, R.J. & STANLEY, M.C. 2005. Human-mediated range expansion of Argentine ants. *Linepithema humile* (Hymenoptera: Formicidae) in New Zealand. *Sociobiology* **45**: 1-7.

WHITE, E.M., WILSON, J.C. & CLARKE, A.R. 2006. Biotic indirect effects: a neglected concept in invasion biology. *Diversity and Distributions* **12**: 443-455.

WITT, A.B.R. 1993. *Factors affecting myrmecochory in fynbos*. MSc Thesis, University of Stellenbosch, Stellenbosch.

WITT, A.B.R. & GILLIOMEE, J.H. 1999. Soil-surface temperatures at which six species of ants (Hymenoptera: Formicidae) are active. *African Entomology* **7**: 161-164.

WITT, A.B.R., GEERTSEMA, H. & GILIOMEE, J.H. 2004. The impact of an invasive ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), on the dispersal of the elaiosome-bearing seeds of six plant species. *African Entomology* **12**: 223-230.

WITT, A.B.R. & SAMWAYS, M.J. 2004. Influence of agricultural land transformation and pest management practices on the arthropod diversity of a biodiversity hotspot, the Cape Floristic Region, South Africa. *African Entomology* **12**: 89-95.

ZAR, J.H. 1984. *Biostatistical analysis*. Prentice-Hall International, Inc.

Table 1. Number of locality records of the Argentine ant in South Africa (SA), based on sampling from the current study, museum records and published literature. N = total number of samples collected. Percentage prevalence in parentheses. All museum records were presences. H = house, G = garden, R = roadside, and O = other. _ = unavailable.

Province name	**Code**	**Current study: N (% prevalence)**					**Museum records: N**	**Published literature: N (% prevalence)**	**Total**
		H	**G**	**R**	**O**	**Total**			
Western Cape	WC	125 (**68.8** %)	103 (**70.8** %)	21 (**52.4** %)	5 (**40** %)	254 (**68.1** %)	49	53 (**43.4** %)	356
Eastern Cape	EC	3 (**33.3** %)	6 (**33.3** %)	1 (**0** %)	0	10 (**30** %)	2	_	12
Northern Cape	NC	3 (**66.7** %)	6 (**33.3** %)	24 (**87.5** %)	0	33 (**75.8** %)	2	_	35
Kwa-zulu Natal	KZN	11 (**0** %)	7 (**0** %)	0	2 (**0** %)	20 (**0** %)	_	_	20
Free State	FS	4 (**50** %)	7 (**57.1** %)	59 (**0** %)	0	70 (**8.6** %)	1	_	71
Mpumalanga	MP	0	0	16 (**0** %)	0	16 (**0** %)	_	1 (**0** %)	17
North West	NW	0	3 (**0** %)	0	0	3 (**0** %)	_	1 (**0** %)	5
Gauteng	GP	15 (**0** %)	52 (**5.8** %)	3 (**0**%)	7 (**0** %)	76 (**3.9** %)	3	_	79
Limpopo	LP	2 (**0** %)	4 (**0** %)	1 (**0** %)	0	7 (**0** %)	1	_	8
Total samples		163	188	125	14	490	58	55	603
Total % prevalence in SA		**55.8** %	**44.7** %	**25.6** %	**14.3** %	**42.7** %			**34.7** %

Table 2. Ant species collected from urban areas and along roadsides in South Africa (SA), with the number of samples occupied by the species in each province. See Table 1 for full province names. * = Tramp species, ** = Invasive tramp species, *# = native to SA, but invasive elsewhere (Passera 1994). All other ant species are native to South Africa. H = House, G = Garden, R = Roadside and O = Other. See http://www.terc.csiro.au/antnames.asp for Alan Andersen's classification of ant common names based on the generic level classification. _ = Common name unknown. Results in this table are based on samples collected for this study only, excluding museum and literature records. Some ant species have several common names, but only one is included in this table.

Species	**Common name**	**Collection habitat (s)**	**Province code (total no. samples collected)**									**No. Provinces occupied**
			EC (10)	**FS (70)**	**GP (76)**	**KZN (20)**	**LP (7)**	**MP (16)**	**NC (33)**	**NW (3)**	**WC (254)**	
Dolichoderinae												
Linepithema humile Mayr**	Argentine ant	H, G, R, O	3	6	3				25		172	**5**
Technomyrmex albipes F. Smith *	White-footed ant	H, G, R	2			3			1		28	**4**
Formicinae												
Anoplolepis custodiens	Pugnaceous ant	H, G, R			1					1	4	**3**
Anoplolepis sp. 1	Pugnaceous ant	G, R		14	1			1			2	**4**
Anoplolepis sp. 2	Pugnaceous ant	H						1			1	**2**
Anoplolepis sp. 3	Pugnaceous ant	G, R		1		1				1		**3**
Anoplolepis sp. 4	Pugnaceous ant	G				1				1		**2**

Species	Common name	Collection habitat (s)	Province code (total no. samples collected)									No. Provinces occupied
			EC (10)	FS (70)	GP (76)	KZN (20)	LP (7)	MP (16)	NC (33)	NW (3)	WC (254)	
Camponotus fulvopilosus Mayr	Sugar ant	H									1	**1**
Camponotus niveosetosus Mayr	Sugar ant	H, G			2	1	1					**3**
Camponotus sp. 2	Pennant ant	H, G, R			20							**1**
Camponotus sp. 3	Pennant ant	G									2	**1**
Lepisiota incisa	_	H, G, R, O	2	3	43	7				1	13	**6**
Lepisiota sp. 1	_	H, R		1	1						3	**3**
Myrmicinae												
Cardiocondyla sp.	_	G									1	**1**
Crematogater sp.	Valentine ant	G				1				1		**2**
Ocymyrmex barbiger Emery	_	G									1	**1**
Pheidole megacephala Mayr*[#]	Brown house ant	H, G, R, O	2	23	37	9	5		3		7	**7**
Pheidole sp. 1	Big-headed ant	G, R						1			1	**2**
Pheidole sp. 2	Big-headed ant	G	1	1		1			1		4	**5**
Pheidole sp. 3	Big-headed ant	G				1	1					**2**

Species	Common name	Collection habitat (s)	Province code (total no. samples collected)									No. Provinces occupied
			EC (10)	**FS (70)**	**GP (76)**	**KZN (20)**	**LP (7)**	**MP (16)**	**NC (33)**	**NW (3)**	**WC (254)**	
Pheidole sp. 4	Big-headed ant	G			2						1	**2**
Pheidole sp. 5	Big-headed ant	R		14								**1**
Tetramorium quadrispinosum Emery	Pennant ant	G, R	1	1	6					1	6	**5**
Tetramorium sp. 1	Pennant ant	G, R			2			1			3	**3**
Tetramorium sp. 2	Pennant ant	H, G, R, O	2	4	7	2	2	1	2	1	5	**9**
Tetramorium sp. 3	Pennant ant	G, R									2	**1**
Tetramorium sp. 4	Pennant ant	G									1	**1**
Tetramorium sp. 5	Pennant ant	G, O			1	2						**2**
Meranoplus sp.	Shield ant	G			1							**1**
Messor capensis Mayr	Harvester ant	G, R		1	2						2	**3**
Messor sp. 1	Harvester ant	H									1	**1**
Messor sp. 2	Harvester ant	H				1						**1**
Monomorium sp.	Mono ant	R			1							**1**
Ponerinae												
Hypoponera sp.	Crypt ant	R									1	**1**

Table 3. Percentage prevalence of all the ant species collected from across the country at various habitats. Total number of samples collected at each habitat in parentheses. H = house, G = garden, R = roadside and O = other. _ = species not collected from that habitat.

Species	**Habitat**				**Total % prevalence**
	H (163)	**G** (188)	**R** (125)	**O** (14)	
Linepithema humile	55.8	44.7	25.6	14.3	**42.7**
Technomyrmex albipes	15.9	3.7	0.8	_	**6.9**
Anoplolepis custodiens	2.5	0.5	0.8	_	**1.2**
Anoplolepis sp. 1	_	1.6	12	_	**3.7**
Anoplolepis sp. 2	1.2	_	_	_	**0.4**
Anoplolepis sp. 3	_	1.1	0.8	_	**0.6**
Anoplolepis sp. 4	_	1.1	_	_	**0.4**
Camponotus fulvopilosus	0.6	_	_	_	**0.2**
Camponotus niveosetosus	0.6	1.6	_	_	**0.8**
Camponotus sp. 2	3.7	4.8	4.0	_	**4.1**
Camponotus sp. 3	_	1.1	_	_	**0.4**
Lepisiota incisa	12.3	20.2	4.0	42.9	**14.1**
Lepisiota sp. 1	2.5	0.8	_	_	**1.0**
Cardiocondyla sp.	0.5	_	_	_	**0.2**
Crematogater sp.	1.1	_	_	_	**0.4**
Ocymyrmex barbiger	0.5	_	_	_	**0.2**

Species	**Habitat**				**Total % prevalence**
	H (163)	**G** (188)	**R** (125)	**O** (14)	
Pheidole megacephala	7.9	15.4	36.8	7.1	**18.2**
Pheidole sp. 1	_	0.5	0.8	_	**0.4**
Pheidole sp. 2	_	4.3	_	_	**1.6**
Pheidole sp. 3	_	1.1	_	_	**0.4**
Pheidole sp. 4	_	1.6	_	_	**0.6**
Pheidole sp. 5	_	_	11.2	_	**2.9**
Tetramorium quadrispinosum	_	6.9	1.6	_	**3.1**
Tetramorium sp. 1	_	1.6	2.4		**1.2**
Tetramorium sp. 2	1.2	7.9	4.8	7.1	**4.9**
Tetramorium sp. 3	_	0.5	0.8	_	**0.4**
Tetramorium sp. 4	_	0.5	_	_	**0.2**
Tetramorium sp. 5	_	1.1	_	7.1	**0.6**
Meranoplus sp.	_	0.5	_	_	**0.2**
Messor capensis	_	1.6	1.6	_	**1.0**
Messor sp. 1	0.6	_	_	_	**0.2**
Messor sp. 2	0.6	_	_	_	**0.2**
Monomorium sp.	_	_	0.8	_	**0.2**
Hypoponera sp.	_	_	0.8	_	**0.2**

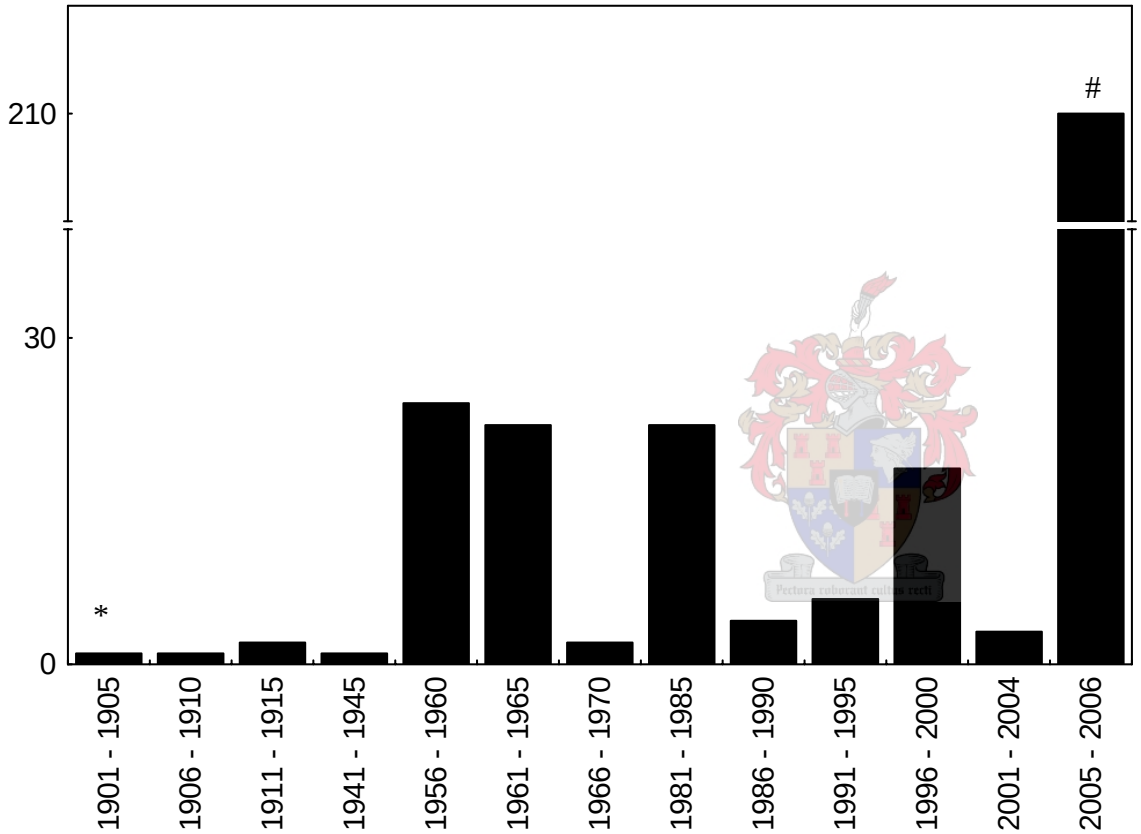


Fig. 1. History of records of the Argentine ant in South Africa. * = first record, # = records from current study

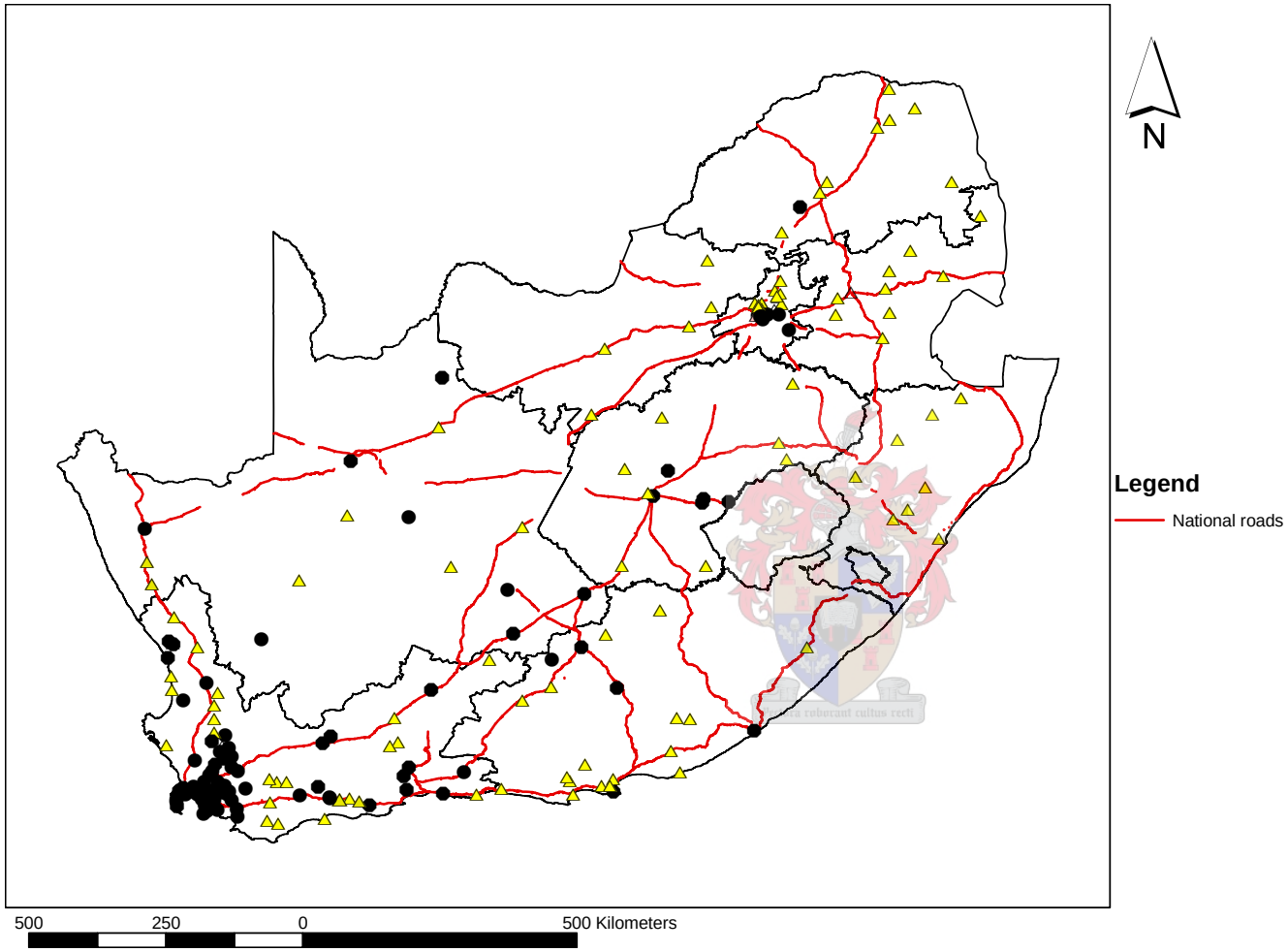


Fig. 2. Current distribution of the Argentine ant in South African urban areas and along roadsides. Closed circles = presence; Yellow triangles = absence.

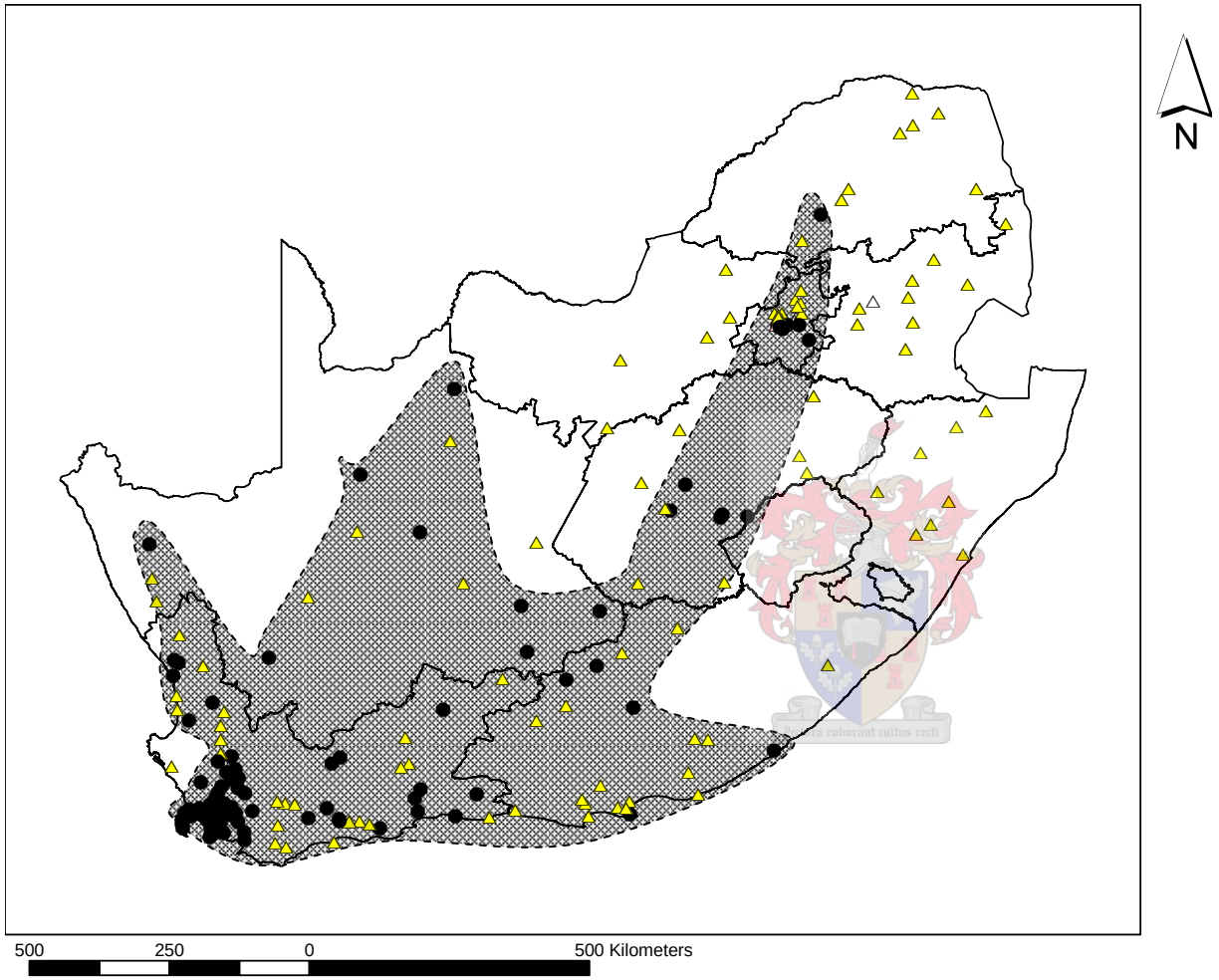


Fig. 3. Extent of occurrence (shaded area) of the Argentine ant in South Africa.

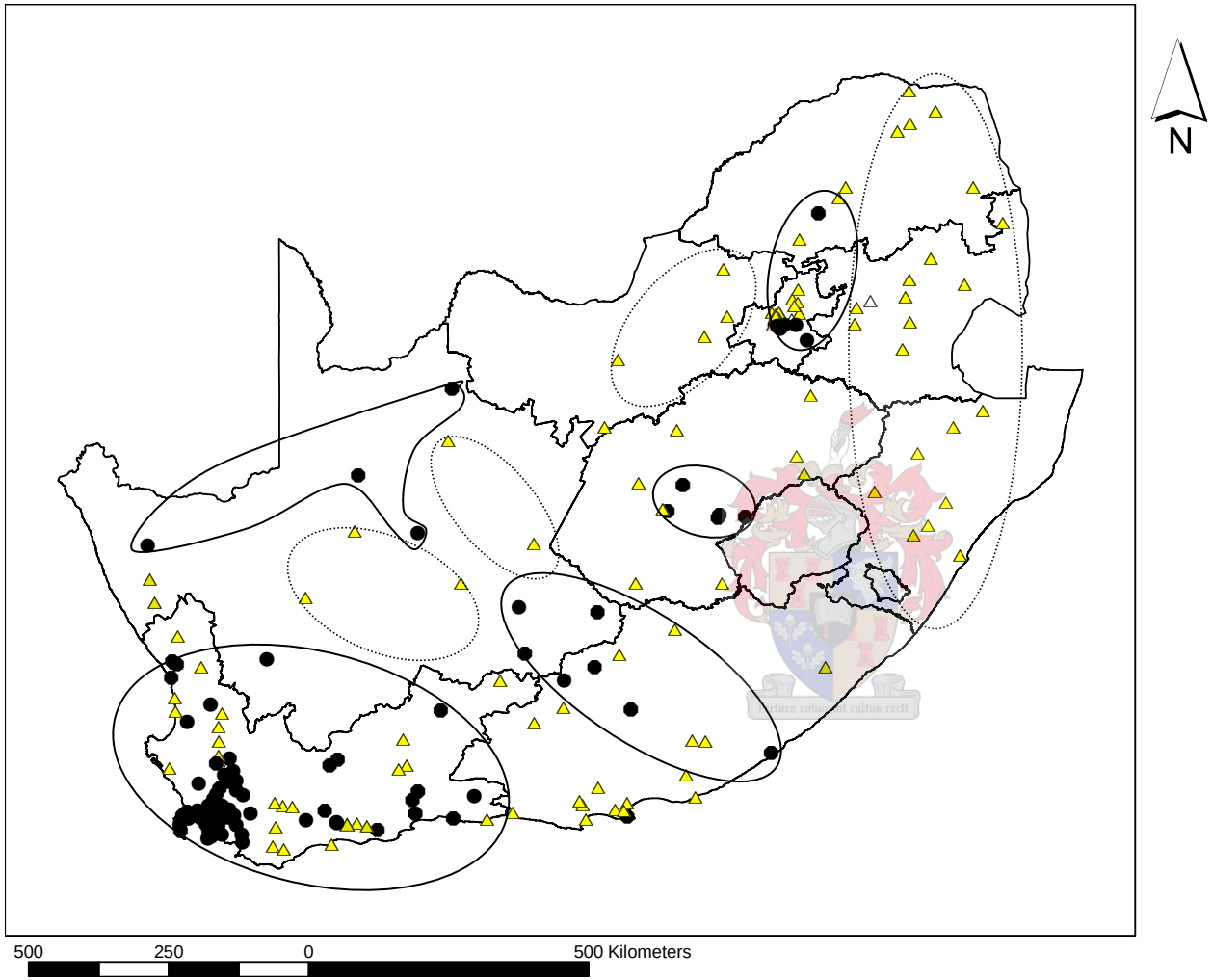


Fig. 4. Estimated perimeters of Argentine ant populations in South Africa. Solid circled = invaded areas; Dashed circles = uninvaded areas.

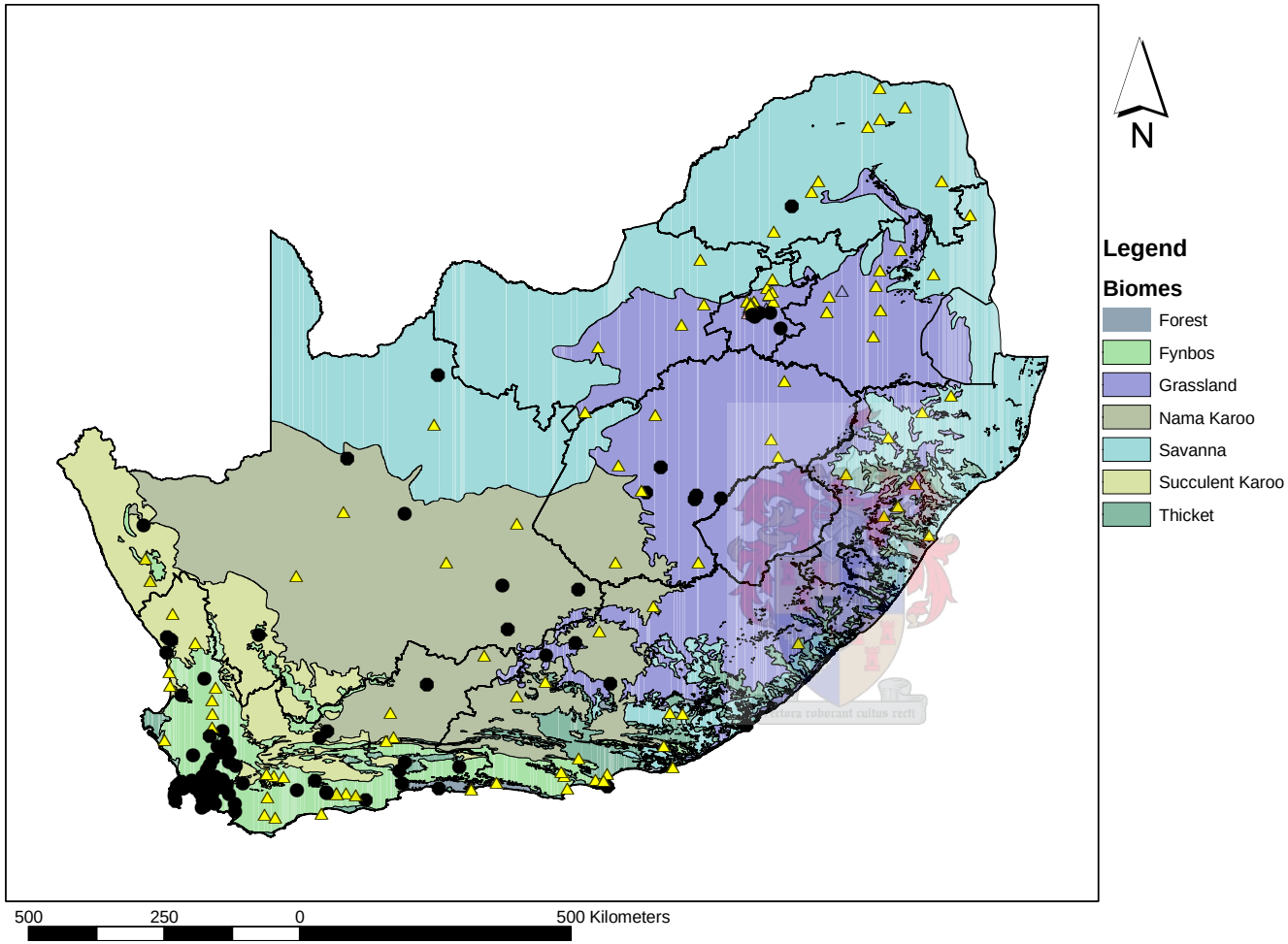


Fig. 5. Distribution of the Argentine ant against a background of biomes (after Rutherford & Westfall 1994) of South Africa. Closed circles = presence; Yellow triangles = absence.

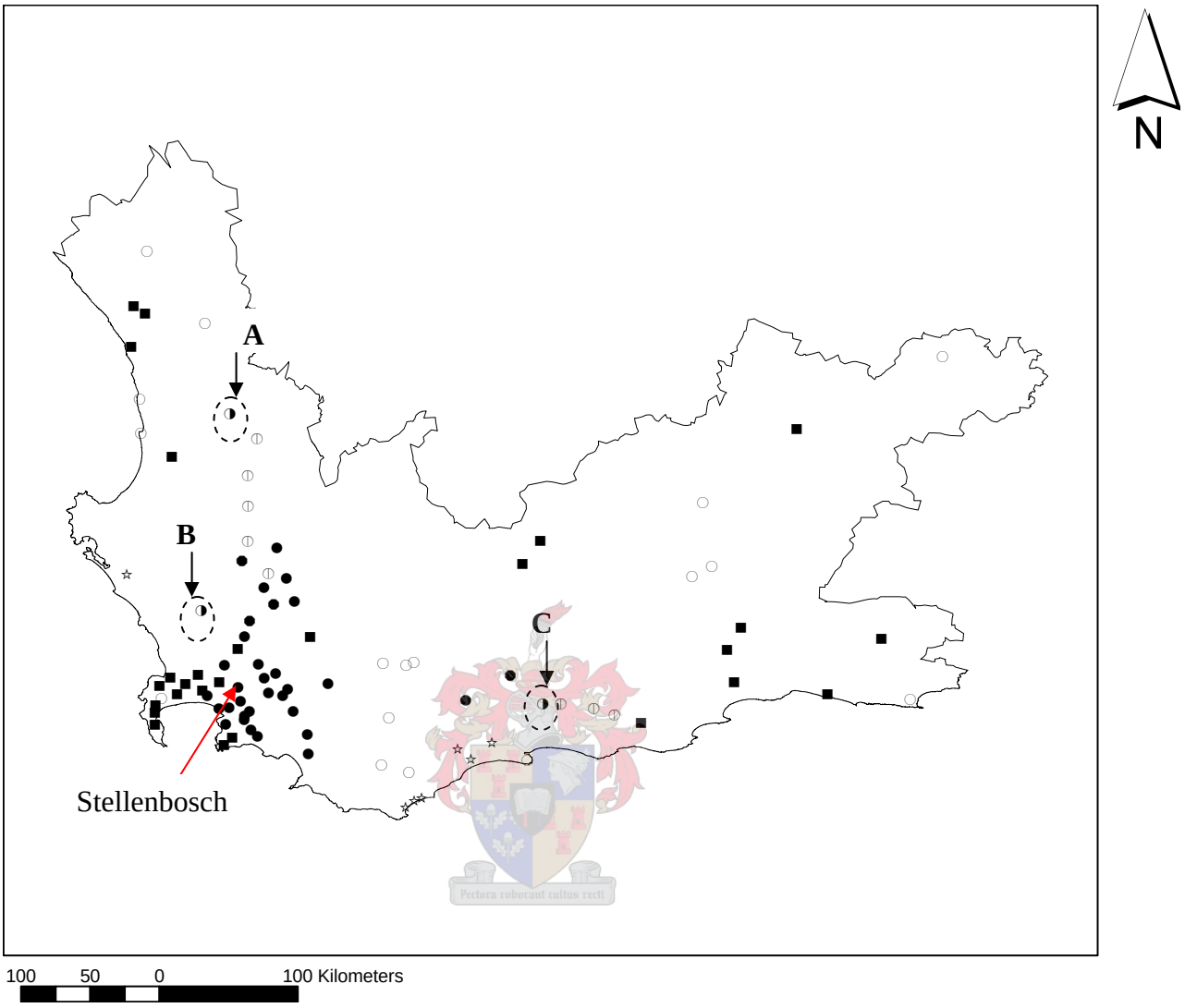


Fig. 6. Current distribution of the Argentine ant in the Western Cape Province, surveyed between 1983 and 1984 (De Kock 1990) and 2005 (current study). Filled circles = present in 1983-1984 and 2005; Divided circles = absent in 1983-1984 and 2005; Filled squares = present in 2005, but data unavailable for 1983-1984; Open circles = absent in 2005, but data unavailable for 1983-1984; Stars = absent in 1983-1984, but data unavailable for 2005. A, B and C = areas where the Argentine ant was absent between 1983 and 1984, but present in 2005.

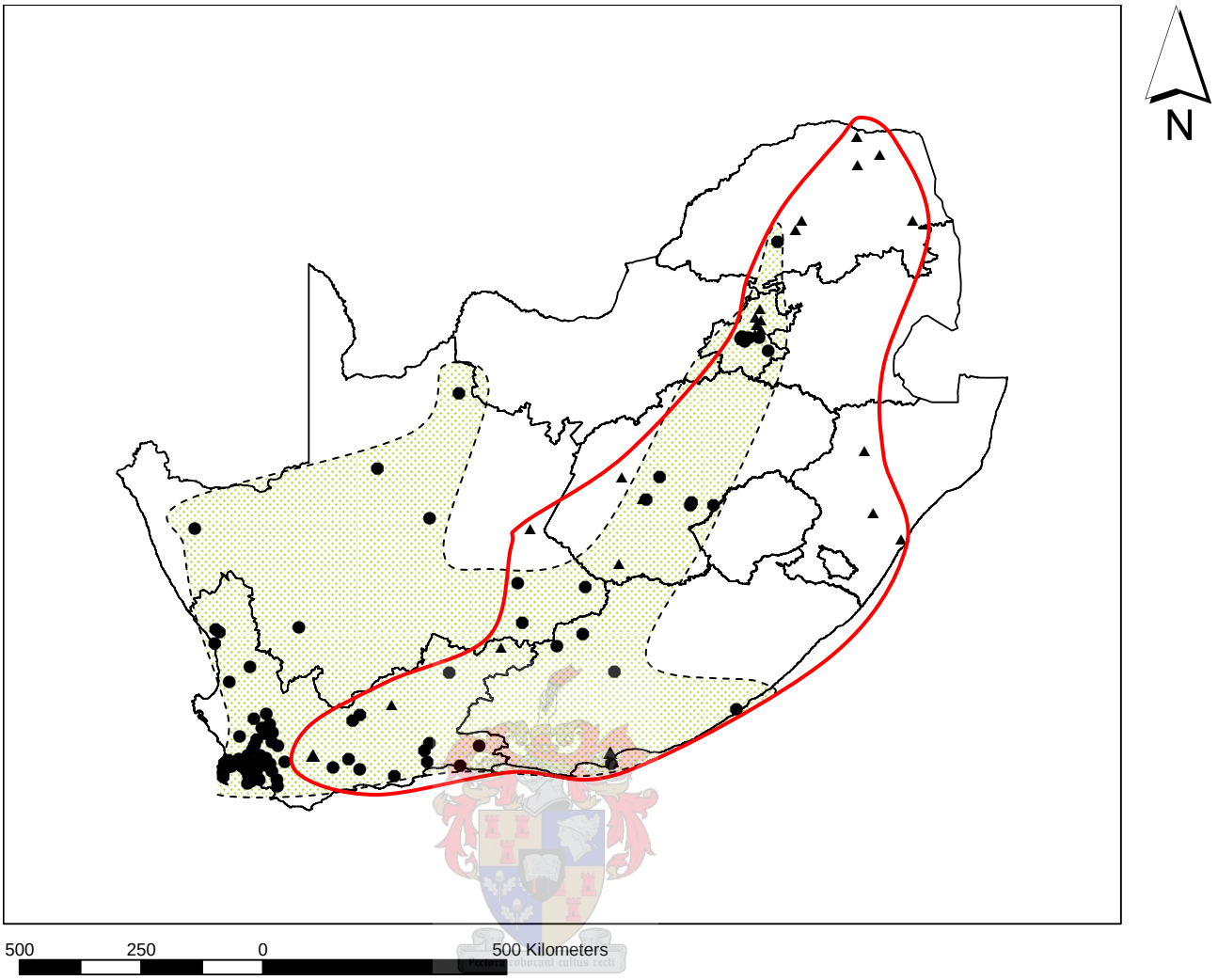


Fig. 7. Distribution of the Argentine ant (closed circles) and the brown house ant (*Pheidole megacephala*) (closed triangles) in South Africa. Shaded area = Argentine ant's extent of occurrence. The red line delineates the brown house ant's extent of occurrence.

.

APPENDICES

Appendix 1. Literature reviewed for the presence and absence of the Argentine ant. WCP = Western Cape Province.

Publication	Study site	Province
Addison & Samways 2000	Vineyards across the WCP	WCP
Bond & Slingsby 1984	Kogelberg Biosphere Reserve	WCP
Boonzaaier 2006	Various nature reserves in the WCP, including Helderberg Nature Reserve	WCP
Botes *et al*. 2006	Greater Cederberg Biodiversity Corridor	WCP
Christian 2001	Kogelberg Biosphere Reserve	WCP
De Kock 1990	Across WCP	WCP
Donnelly & Giliomee 1985	Jonkershoek Nature Reserve	WCP
Parr *et al*. 2002	Pilanesberg National Park	North West Province
Parr *et al*. 2004	Kruger National Park	Mpumalanga
Van Hamburg *et al*. 2004	Hendrina Power Station	Mpumalanga
Witt 1993	Jonkershoek Nature Reserve	WCP
Witt *et al*. 2004	Jonkershoek Nature Reserve	WCP
Witt & Samways 2004	Elgin Experimental Farm, Garbouw	WCP

Appendix 2. An information sheet that was included in each sampling kit, containing a 1.5 ml epindof tube half-filled with 100 % ethanol.

Argentine Ant Information Sheet

The Argentine Ant (*Linepithema humile* Mayr*)* was inadvertently introduced into South Africa in the early 1900's. It is now thought to have spread through much of the Western Cape Province, but its distribution in South Africa is not well known. It is commonly found in association with humans, in houses and in agricultural areas (and is considered a pest in vineyards). This ant has in fact invaded several parts of the world, and has a significant negative effect on biodiversity. For example, it forms extremely large colonies that outcompete local ant species. This disrupts important interactions between native ant and plant species in the Fynbos (ants are responsible for dispersing the seeds of several Fynbos plants).

What to do!

You can make a valuable contribution to this research by sampling between 1-10 ant individuals from your home or garden and placing them inside the tube provided. Please seal the tube in the envelope, complete the form on the front of the envelope and return to the researcher. (The tube contains laboratory grade alcohol and skin contact is not harmful.) If you collect ants from more than one residence (e.g. from a holiday house or on a weekend away), or from your home and garden, please use a separate tube or sampling kit for each.

Enquiries contact: Ndivhuwo or Melodie at 021 808 2635

Thank you for your assistance

Appendix 3. A label that was attached on the outside of each sampling kit with information required from the collector.

Argentine Ant Project

Name of collector: _____

Date: _____

Address/locality of ants collected:_____

House/garden/other?_____

Contact details (optional)_____

Would you like feedback? Yes____ No____

CHAPTER 5

General conclusion

Human activities, particularly global trade and transportation continue to introduce many species of different taxa into various parts of the world outside their native ranges (Drake *et al*. 1989; McGlynn 1999; Ward *et al*. 2006). However, not all introduced species become invasive, some never establish and others never spread to become invasive (Lodge 1993; Von Aesch & Cherix 2005; Von Holle & Simberloff 2005). Environmental factors, as well as characteristics of the introduced species play a major role in determining the chances of survival of the species (Krushelnycky *et al*. 2005). High propagule pressure (a measure of how often a species is introduced to areas outside its native range (Lockwood *et al*. 2005)) may also increase the chance of successful establishment of a non-native species (Alpert 2006; Colautti *et al*. 2006). Unfortunately, most of the species that do become invasive often have devastating consequences on the ecological systems of the invaded communities (Vitousek *et al*. 1997; Holway *et al*. 2002). Here, the current distribution range of the Argentine ant in South African urban areas and inside protected areas was quantified. In addition, the impact of this species on the local ant fauna was assessed.

The most striking result of this study was that almost half of South Africa's land surface area includes urban sites invaded by the Argentine ant, and that range expansion is occurring predominantly via human-mediated jump dispersal. It was therefore evident that this species is well established in South Africa. The presence of human-influenced landscapes such as buildings and picnic sites play a great role in influencing the distribution and spread of the Argentine ant at both national scale (across the country) and at local scale (within a reserve). Although studies conducted elsewhere in the world, particularly in California, demonstrated that soil moisture (Menke & Holway 2006) and the availability of permanent watercourses (Ward 1987; Espadaler & Gomez 2003) influences the distribution of this species, results of this study did not support this hypothesis. The majority of the Argentine ant introductions into protected areas appear to occur at low altitude areas, where most human-modified habitats are situated. Thus, low altitude areas have higher invasion rates than high altitude areas, although this study demonstrated that the Argentine ant can also establish successfully at high altitudes if introduced there by humans. The natural rate of spread for the Argentine ant in this study was very slow, consistent with the natural rate of spread shown elsewhere in the world (Erickson 1971; Holway 1995). Invasion of protected areas by the Argentine ant has resulted in severe biotic homogenization of the local ant fauna, and only a small proportion of the native ant community is able to resist displacement. The increase in the distribution range of

the Argentine ant inside protected areas and across the country could result in the displacement of more native ant species from invaded areas.

Strategies for the long-term control and management of the Argentine ant in natural areas have so far not been successful (Soeprono & Rust 2004). Control measures should therefore focus more on preventing new introductions or eradicating new populations rather than focusing on established populations (Moody & Mack 1988; Suarez *et al*. 2001). Previous studies have shown that with the change in climate, many more places around the world are likely to become suitable for the Argentine ant invasion (Roura-Pascual *et al*. 2004; Hartley *et al*. 2006), thereby increasing its global distribution range. Despite its widely reported preference for areas with a Mediterranean and sub-tropical climate (Suarez *et al*. 2001), it is highly likely that in time, the non-Mediterranean areas of South Africa and elsewhere in the world, will be invaded by the Argentine ant. Effective preventive measures are therefore necessary to prevent the spread of this species, particularly inside protected areas.

In conclusion, this study provides valuable baseline information regarding the extent of the Argentine ant invasion in South African urban areas as well as inside protected areas, and also provides information on habitat-specific associations. Thus, data obtained here provides information on where this species occurs, and this information can be useful in the management of this species, particularly inside protected areas. Since the Argentine ant clearly prefers disturbed areas, it is recommended that to limit the spread of this species, any future development of recreational areas inside protected areas, particularly buildings, should be limited to one point rather than scattered throughout the reserve, and these buildings should preferably be closer to the edge of the protected area.

FUTURE RESEARCH

Although the distribution range of the Argentine ant inside the three protected areas has been determined here, the change in this distribution range should be monitored regularly. This will be useful in determining the rate of spread of this species within these reserves. Factors that limit the distribution of the Argentine ant inside protected areas, e.g. biotic resistance by native ant species, should be explicitly tested. In addition, the impact of soil type on the distribution of the Argentine ant should be assessed. Strategies for eliminating the Argentine ant from natural areas have proven unsuccessful elsewhere in the world, however, ways to limit further spread of this species within protected areas should be explored. Human activities that promote introduction of the Argentine ant into new areas should be identified,

i.e. products that carry a complete nest (both workers and queens) from one province to another.

Evidently, more research is needed to help understand the severity of the Argentine ant invasion in South Africa, particularly its direct and indirect impact on other invertebrates. Understanding the various aspects, i.e. biotic and abiotic factors that contribute to the Argentine ant invasion will be a great improvement towards the successful management of this species in South Africa.

REFERENCES

ALPERT, P. 2006. The advantages and disadvantages of being introduced. *Biological Invasion* **8**: 1523-1534.

COLAUTTI, R.I., GRIGOROVICH, I.A. & MACISAAC, H.J. 2006. Propagule pressure: a null model for biological invasions. *Biological Invasions* **8**: 1023-1037.

ERICKSON, J.M. 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. *Psyche* **78**: 257-266.

ESPADALER, X. & GÓMEZ, C. 2003. The Argentine ant, *Linepithema humile*, in the Iberian Peninsula. *Sociobiology* **42**: 187-192.

DRAKE, J.A., MOONEY, H.A, DI CASTRI, H.A., GROVES, F., KRUGER, F.J., REJMANEK, M. & WILLIAMSON, M. 1989. *Biological invasions: a global perspective*. John Wiley & Sons. New York.

HARTLEY, S., HARRIS, R. & LESTER, P.J. 2006. Quantifying uncertainty in the potential distribution of an invasive species: climate and the Argentine ant. *Ecology Letters* **9**: 1068-1079.

HOLWAY, D.A. 1995. Distribution of the Argentine ant (*Linepithema humile*) in Northern California. *Conservation Biology* **9**: 1634-1637.

HOLWAY, D.A., LACH, L., SUAREZ, A.V., TSUTSUI, N.D. & CASE, T.J. 2002. The causes and consequences of ant invasions. *Annual Review of Ecological Systematics* **33**: 181-233.

KRUSHELNYCKY, P.D., JOE, S.M., MEDEIROS, A.C., DAEHLER, C.C. & LOOPE, L.L. 2005. The role of abiotic conditions in shaping the long-term patterns of a high-elevation Argentine ant invasion. *Diversity and Distributions* **11**: 319-331.

LOCKWOOD, J.L., CASSEY, P. & BLACKBURN, T. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* **20**: 223-228.

LODGE, D.M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* **8**: 133-137.

MCGLYNN, T.P. 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography* **25**: 535-548.

MENKE, S.B. & HOLWAY, D.A. 2006. Abiotic factors control invasion by Argentine ants at the community scale. *Journal of Animal Ecology* **75**: 368-376.

MOODY, M.E. & MACK, R.N. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* **25**: 1009-1021.

ROURA-PASCUAL, N., SUAREZ, A.V., GÓMEZ, C. PONS, P., TOUYAMA, Y., WILD., A.L. & PETERSON, T. 2004. Geographical potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. *Proceedings of the Royal Society of London B.* **271**: 2527-2534.

SOEPRONO, A.M. & RUST, M.K. 2004. Strategies for controlling Argentine ants (Hymenoptera: Formicidae). *Sociobiology* **44**: 669-682.

SUAREZ, A.V., HOLWAY, D.A. & CASE, T.J. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proceedings of the National Academy of Science* **98**: 1095-1100.

VITOUSEK, P.M., D'ANTONIO, C.M., LOOPE, L.L., REJMÁNEK, M. & WESTBROOKS, R. 1997. Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* **27**: 1-16.

VON AESCH, L. & CHERIX, D. 2005. Introduced ant species and mechanisms of competition on Floreana Island (Galápagos, Ecuador). *Sociobiology* **45**: 1-19.

VON HOLLE, B. & SIMBERLOFF, D. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* **86**: 3212-3218.

WARD, P.S. 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento Valley and its effects on the indigenous ant fauna. *Higardia* **55**: 1-16.

WARD, D.F., BEGGS, J.R., CLOUR, M.N., HARRIS, R.J. & O'CONNOR, S. 2006. The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal. *Diversity and Distributions* **12**: 601-609.